UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PASSER LA SYLVICULTURE DANS LA TORDEUSE : ÉVALUATION DES TRAITEMENTS PRÉVENTIFS FACE AUX PERTES DE BOIS LIÉES À LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE.

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Le premier article est intitulé : « ESTIMATING FOREST VULNERABILITY TO THE NEXT SPRUCE BUDWORM OUTBREAK: WILL PAST SILVICULTURAL EFFORTS PAY DIVIDENDS? ». Les coauteurs sont Daniel Kneeshaw, David MacLean et Chris Hennigar. Cet article est publié dans la revue canadienne de recherche forestière.

Le deuxième article est intitulé : « FOREST HARVESTING AND SPRUCE BUDWORM OUTBREAKS CAUSE SIMILAR SHIFTS IN SPECIES DOMINANCE ». Les coauteurs sont Daniel Kneeshaw et David MacLean. Cet article est en préparation pour soumission à la revue *Forests*.

Le troisième article est intitulé : « EFFECTIVENESS OF PREVENTIVE FOREST MANAGEMENT STRATEGIES IN REDUCING THE SEVERITY OF SIMULATED SUCCESSIVE SPRUCE BUDWORM OUTBREAKS ». Les coauteurs sont Daniel Kneeshaw, David MacLean et Brian Sturtevant. Cet article est en préparation pour soumission à la revue *Forest Ecology and Management*.

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RÉSUMÉ DE LA THÈSE

Il est généralement attendu qu'au Québec, l'épidémie en cours sera moins sévère que la dernière. Cette croyance se base sur deux raisons principales: le jeune âge des peuplements de sapin actuels réduisant leur vulnérabilité et la proportion croissante d'espèces feuillues dans les sapinières, les feuillus étant reconnus pour créer un effet protectif contre la défoliation par la TBE par le biais d'une plus grande abondance d'ennemis naturels et de barrière potentielle à la dispersion de la TBE. Plusieurs modifications de la composition et de la structure sont survenues dans les dernières décennies et les traitements sylvicoles préventifs, principalement des manipulations de composition, appliqués depuis la dernière épidémie de TBE font partie de ces changements. Or, l'ampleur et les effets de ces manipulations de composition demeurent méconnus. Afin d'évaluer l'efficacité des traitements préventifs face aux dommages potentiels par la TBE, nous avons analysé l'historique de perturbation récent d'un secteur intensivement aménagé de la Gaspésie. Nous avons utilisé les données de la base de données SIFORT et simulé les effets d'épidémies de TBE afin de déterminer la vulnérabilité de la forêt à partir des conditions forestières observées tôt dans la dernière épidémie de TBE (1985) et 12 ans après cette dernière (2004). Les résultats de ces simulations ont montré que l'approche visant à augmenter l'abondance d'épinette noire est la plus efficace pour diminuer les pertes en volume liées à la TBE, mais que d'importants efforts de gestion de la végétation compétitrice sont nécessaires dans ces peuplements. Par ailleurs, nous avons également observé une importante régénération feuillue suite à l'épidémie de TBE, mais également suite à la récolte de bois.

La question de la durabilité de l'aménagement forestier est donc apparue importante suite aux signes de perte de rendement en bois résineux observés en Gaspésie. Nous avons alors analysé les changements de composition après TBE et coupe forestière le long d'un gradient longitudinal de la sapinière du Québec, dans 3 sites allant d'un climat continental, où les feuillus dominent, à un climat maritime, où le sapin baumier domine. Les analyses ont été effectuées à partir de la base de données SIFORT, où les inventaires de 1972-74 et ceux de 2004-2006 ont été comparés en termes de composition. Les résultats montrent que l'important enfeuillement observé, particulièrement en Gaspésie, est probablement localisé et temporaire, dû à la prédominance du modèle successionnel alternant entre dominance mixte et sapin dans cette région dominée par le sapin baumier avant la dernière épidémie de TBE. Par ailleurs, la composition régionale s'est avérée un facteur important pour prédire la succession après perturbation, qui est apparue très similaire tant après coupe qu'après TBE. Les coupes forestières ne seraient donc pas la principale cause d'enfeuillement depuis la dernière épidémie, allant jusqu'à améliorer le rendement résineux après coupe dans les régions à forte proportion de feuillus.

À plus long terme, la question de la dynamique de perturbation se complexifie en considérant la succession d'épidémies de TBE et la suite de traitements sylvicoles en parallèles. Les résultats obtenus précédemment provenant d'un contexte d'épidémie unique, nous avons poussé l'évaluation des différentes approches de sylviculture préventive et effectué des simulations d'aménagement pour des séries de trois épidémies successives à partir du modèle de dynamique forestière LANDIS-II, implémenté sur un territoire du centre du Québec. Nos simulations d'aménagement intensif d'épinette à long terme ont montré une grande efficacité à diminuer la vulnérabilité à grande échelle, mais dans ce cas, une gestion de la végétation efficace était essentiellement implicite dans le modèle, compte tenu du faible envahissement par la végétation compétitrice par rapport à ce que nous avons observé au Québec depuis la dernière épidémie. L'aménagement extensif (sans plantation ou éclaircie), en permettant le maintien de feuillus après coupe, s'est également avéré efficace dans l'ensemble pour réduire la vulnérabilité des forêts, mais son efficacité à augmenter le rendement résineux après épidémie dépendrait largement de la composition avant coupe.

Cette thèse montre donc que l'approche préventive s'avère globalement efficace, mais que le contexte local et régional doit être tenu en compte et que cet aménagement doit, par conséquent, être utilisé avec précaution. De surcroît, il faudrait possiblement concentrer les efforts d'aménagement intensif sur un nombre plus restreint de peuplements afin de limiter la végétation compétitrice, potentiellement où les gains seraient les meilleurs, donc dans les secteurs les plus productifs. Il en ressort donc que l'aménagement tel que pratiqué actuellement, avec sa diversité de traitements ayant des avantages différents et complémentaires, n'est pas si mauvais en soi d'un point de vue général. Ces aspects, parallèlement à la redéfinition des traitements sylvicoles pour optimiser la quantité de feuillus et augmenter leur efficacité, constituent sans aucun doute les principales recommandations à tirer de cette thèse.

MOTS-CLÉS : Tordeuse des bourgeons de l'épinette, sylviculture, aménagement extensif, protection des forêts, succession forestière, vulnérabilité des forêts, effet de protection des feuillus.

INTRODUCTION GÉNÉRALE

La tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) est un insecte défoliateur indigène à la forêt boréale d'Amérique du Nord et représente l'un des ravageurs forestiers les plus dommageables du Canada. De 1978 à 1987, la tordeuse des bourgeons de l'épinette (TBE) a généré des pertes de croissance et une mortalité équivalant à environ 32 × 106 à 43 ×106 m3/année à travers l'Est du Canada (Power 1991). Elle se nourrit principalement du sapin baumier (*Abies balsamea* (L.) Mill.), mais affecte également l'épinette blanche (*Picea glauca* (Moench) Voss), rouge (*Picea rubens* Sarg.) et noire (*Picea mariana* (Mill.) B. S. P.) dans une moindre mesure (Hennigar et al. 2008). Les facteurs déterminant ses préférences sont multiples, mais incluent principalement le synchronisme phénologique des espèces et les caractéristiques du feuillage (Mattson et al. 1983; Hennigar et al. 2008). Les épidémies de TBE affectent de grands territoire (58 Mha au pic de la dernière épidémie (Kettela 1983)) et reviennent selon un cycle approximatif de 30-40 ans (Blais 1983; Boulanger et Arseneault 2004).

Pendant le dernier siècle, trois épidémies de TBE majeures ont eu lieu au Québec, la dernière ayant eu lieu de 1967 à 1992 (Ressources naturelles et faune Québec 2010). La plupart des forêts susceptibles à la TBE sont régulièrement affectées par des épidémies, mais dont la sévérité varie d'une épidémie à l'autre (Blais 1983). Une épidémie est actuellement en cours au Québec, principalement sur la Côte-Nord, et bien que ce secteur ait été peu affecté lors de la dernière épidémie, il est généralement attendu qu'ailleurs au Québec, l'épidémie en cours sera moins sévère que la dernière. Cette croyance se base sur deux raisons principales: le jeune âge des peuplements de sapin actuels réduisant leur vulnérabilité (Blais 1981) et la proportion croissante d'espèces feuillues dans les sapinières, telles que le bouleau blanc (*Betula papyrifera* Marshall), le bouleau jaune (*Betula alleghaniensis* Britton) et le peuplier faux-tremble (*Populus tremuloides* Michx.), (Bouchard et al. 2006), les feuillus étant reconnus pour créer un effet protectif contre la défoliation par la TBE (Su et al. 1996; Campbell et al. 2008) par le biais d'une plus grande abondance d'ennemis naturels (Cappuccino et al. 1998) et de barrière potentielle à la dispersion de la TBE. Cette perspective est partagée par les aménagistes, qui planifient déjà en prévision d'une épidémie à venir de faible sévérité (James W. Sewall Company 2011), ignorant les risques liés au fait que ces attentes demeurent plus qu'incertaines.

Beaucoup d'incertitude demeure également quant à la dynamique des épidémies de TBE dans le paysage de plus en plus aménagé qu'est la forêt boréale, d'autant plus que cette dynamique implique de grandes échelles spatiales et temporelles. Les conséquences des legs de l'aménagement forestier sur le régime d'épidémie de TBE et sur les pertes de bois futures font partie des problématiques à investiguer. Bien que notre faible compréhension de la dynamique des épidémies de TBE nuit à la fiabilité des prédictions des caractéristiques d'épidémie futures, il est néanmoins reconnu que les activités d'aménagement telles que la coupe et la suppression des feux ont modifié les caractéristiques du couvert forestier et du régime d'épidémies de TBE (Blais 1983; Anderson et al. 1987; Robert et al. 2012). Parallèlement, un rallongement du cycle de feu (Bergeron and Archambault 1993) est également pointé du doigt pour expliquer l'augmentation de l'abondance du sapin baumier en forêt boréale de l'Est du Canada, suggérant une combinaison de facteurs causaux (Bergeron and Leduc 1998).

À l'inverse, plusieurs ont suggéré qu'il est possible que cette interaction entre l'aménagement forestier et la TBE soit mise à profit afin de rendre le couvert volontairement moins vulnérable à la TBE au moyen d'une sylviculture préventive (Blais 1964; Gagnon et Chabot 1991; MacLean 1996). Parmi les méthodes proposées, on retrouve : la détermination de priorités de récoltes des peuplements plus vulnérables (MacLean et al. 2001), des modifications à la composition forestière au moyen de plantation d'espèces peu, voire non-vulnérables, et au moyen d'éclaircie précommerciale diminuant l'abondance du sapin et au moyen du maintien d'espèces feuillus diminuant la défoliation des espèces hôtes, de même que la diminution de l'âge des peuplements vulnérables (MacLean 1996; Chabot et al. 2013). Ces interactions entre l'aménagement forestier et la dynamique des épidémies de TBE sont réunies dans la littérature dans ce qu'on appelle l'hypothèse sylvicole, qui demeure toutefois un sujet controversé vu les nombreux trous dans la connaissance (Miller et Rusnock 1993). Entres autres, plusieurs ont recommandé les éclaircies comme moyen de prévention face à la TBE (Blum and MacLean 1984; Bauce 1996), mais cette stratégie demeure hautement controversée compte tenu de la littérature contradictoire (Batzer et al. 1987; Moreau et al. 2006) et du manque d'expérimentation à grande échelle (Miller and Rusnock 1993).

Les sections suivantes approfondissent deux thèmes majeurs liés à la problématique de l'aménagement forestier dans un contexte d'épidémies de TBE et les principaux thèmes abordés dans cette thèse, soit ceux de l'impact des traitements sylvicoles et de leur intégration dans les modèles de prévisions de rendement forestier devenus dorénavant essentiels dans la planification de l'aménagement forestier. Ces thèmes font tous référence à des notions de foresterie, dont en voici une description sommaire :

Aménagement forestier : Branche de la foresterie concernée par les aspects administratifs, économiques, légaux, sociaux, scientifiques, techniques et plus particulièrement de la silviculture, de la protection et de la législation forestière (Helms 1998).

Aménagement forestier extensif : Stratégie d'aménagement qui repose sur la régénération naturelle et la protection contre les incendies et les insectes (Sauvageau 1995).

Aménagement forestier intensif : Stratégie d'aménagement forestier à laquelle s'ajoutent les soins culturaux aux jeunes peuplements et la régénération des peuplements par des moyens artificiels (Sauvageau 1995).

Aménagement forestier préventif : (ou approche ou stratégie préventive) Stratégie de protection des forêts visant à réduire les risques de perturbation naturelles avant leur apparition. Comprends des traitements tels que les manipulations de composition (incluant les traitements d'aménagement forestier intensif) et de structure d'âge pour réduire la vulnérabilité des forêts face à la tordeuse des bourgeons de l'épinette. Le terme fait opposition à celui d'aménagement réactif, où les mesures sont prises une fois la perturbation en cours (e.g. arrosage aérien d'insecticide pour contrer un ravageur forestier).

Sylviculture : Aménagement et étude des peuplements forestiers en vue de produire des attributs et produits désirés (Puettman et al. 2009).

Sylviculture intensive : Ensemble des pratiques sylvicoles dans les peuplements [...] afin d'en améliorer la valeur et le rendement (Sauvageau 1995).

L'aménagement forestier dans un contexte d'épidémie

L'approche de gestion des impacts de la TBE généralement adoptée est plutôt réactive, au moyen de coupes de récupération des peuplements affectés par la mortalité, d'application d'insecticide visant à protéger le feuillage dans les peuplements les plus vulnérables (Hudak 1991; Coulombe et al. 2004), ou de réajustements fréquents à la planification des récoltes (Erdle et Ward 2008). Par contre, ces méthodes réactives ne permettent généralement de protéger qu'une minorité des pertes liées à la TBE, tel que démontré par la récente épidémie de dendroctone du pin ponderosa dans l'Ouest de l'Amérique du Nord où de grandes quantités de bois ont été perdues (Coops et al. 2008; Schneider et al. 2010). Par ailleurs, le bois issu des coupes de récupération, dont le taux d'humidité est inférieur au bois sain, ne correspond généralement pas aux standards d'humidité du bois des usines de transformation qui se voient forcées de le transformer par la législation. Quant à lui, l'épandage d'insecticide, bien qu'efficace pour diminuer la défoliation (MacLean et al. 2001; Fournier et al. 2010), demeure un traitement dispendieux.

L'approche préventive apparaît donc potentiellement plus efficace et plus rentable (Cayuela et al. 2011) et d'importants investissements sont déjà alloués par les aménagistes afin de mettre en application cette stratégie (James W. Sewall Company 2011; Chabot et al. 2013), dont fait également partie la stratégie de protection des forêts appliquée au Québec (Gouvernement du Québec 2000). Parmi les traitements préventifs, principalement des manipulations de composition, on retrouve la plantation d'espèces peu ou pas affectées par la TBE, e.g. l'épinette noire, la réduction de l'abondance du sapin par la coupe ou l'éclaircie précommerciale et la promotion du contenu en feuillus (Cappuccino et al. 1998; Muzika et Liebhold 2000). Bien que l'effet des plantations d'espèces non-hôtes sur le rendement résineux apparaît relativement prévisible à moyen terme, différents cas de dérapages non-désirés des systèmes écologiques ont été rapportés à plus long terme (Pureswaran et al. 2015), rappelant qu'une approche trop contrôlante rapportée à grande échelle peut aussi avoir des effets néfastes sur la dynamique forestière et conséquemment sur la récolte de bois (Holling et Meffe 1996). Essentiellement, la validité de l'hypothèse sylvicole sur le terrain demeure méconnue et plusieurs suggèrent d'approfondir nos connaissances à ce chapitre avant d'y investir davantage de temps et d'argent (Miller et Rusnock 1993).

L'effet lié à une présence accrue des feuillus après coupe devient également complexe à analyser, considérant leur effet à la fois positif, sur la protection face à la défoliation, et à la fois négatif, sur la diminution de l'espace alloué à la croissance des résineux. Cette dualité dans l'impact de la présence de feuillus sur la production résineuse, d'abord évaluée par Su et al. (1996), a ensuite été approfondie afin de déterminer une proportion de feuillus optimale maximisant l'effet protecteur et le rendement résineux (Needham et al. 1999). Cette proportion dépendrait de la sévérité des épidémies, allant d'aucun gain en résineux liés au contenu en feuillu en deçà de 45% de défoliation (période de 5 ans) à un gain optimal en résineux dans les peuplements à 50% de feuillus lors de période où la défoliation excède 85% (18% de pertes en volume vs. 95% pour les sapinières pures). Or la durée des épidémies s'allonge généralement au-delà de 5 ans et il est rare qu'une défoliation aussi forte affecte un paysage entier. Il existe donc un besoin de connaître l'effet net des feuillus sur la production résineuse à grande échelle afin d'évaluer l'efficacité de l'approche passive d'augmentation des feuillus par l'aménagement traditionnel pour augmenter les rendements résineux.

L'approche traditionnelle d'aménagement forestier dite extensive est caractérisée par différents types de coupes dont l'intensité est variée, mais elle mise avant tout sur la régénération naturelle pour assurer le maintien du couvert forestier (Benson 1990). En sapinière, cette régénération est souvent dominée par le sapin, dont la régénération sous-couvert génère fréquemment une dynamique de succession dite autogénique, ou cyclique (Frelich et Reich 1995), où le couvert mature de sapin présent avant perturbation laisse éventuellement place à un autre couvert dominé par le sapin (Baskerville 1975; Morin 1994). Les décennies d'aménagement forestier extensif ont d'ailleurs été pointées du doigt pour avoir augmenté la teneur en sapin des sapinières québécoises (Blais 1983). Or, il apparaît qu'autant dans les secteurs aménagés (Harvey et Bergeron 1989) que ceux affectés par la TBE (Bouchard et al. 2006), l'ouverture du couvert peut également favoriser la régénération feuillue, générant ainsi un couvert plus mixte qu'avant perturbation. Une combinaison de facteurs favoriserait le retour accru d'espèces feuillues, dont des facteurs liés aux sites (bon drainage, microclimat plus chaud, grande taille de trouées (Bouchard et al. 2006)) et à la sévérité des épidémies, étant donné la régénération feuillue favorisée dans les cas d'épidémies sévères où la mortalité affecte également les sapins en régénération (Ruel et Huot 1993). Dans les secteurs aménagés, la grande taille des blocs de coupes totales de même que le passage de la machinerie, stimulant la reproduction végétative des feuillus intolérants, font partie des facteurs permettant un retour accru des feuillus après coupe (Harvey et Bergeron 1989). Cette présence de feuillus après passage de la TBE demeure toutefois temporaire et la dominance par le sapin réapparaît à mesure que les feuillus du couvert dominant meurent, générant par le fait même une dynamique d'alternance entre un couvert à dominance mixte et un autre à dominance de sapin (Holling 1973).

Les peuplements mixtes ont pris de l'importance dans toute la sapinière du Québec depuis la dernière épidémie (Labbé et al. 2009), suggérant que le modèle d'alternance ait été plus important que le modèle autogénique. Cet effet se traduit donc par une augmentation de feuillus, tant à l'échelle du peuplement qu'à l'échelle du paysage. La situation est semblable dans les peuplements non-aménagés du Nouveau-Brunswick, territoire également très affecté par la TBE, où les feuillus ont pris plus d'importance depuis la moitié du 20e siècle (Etheridge et al. 2005; Amos-Binks et al. 2010). Bien que cette dernière épidémie ait été particulièrement sévère et étendue, il appert également que la sapinière n'a jamais été aussi aménagée qu'elle ne l'est actuellement; il devient donc difficile de déterminer la cause de cette présence feuillue accrue en sapinière. Cette question s'avère importante d'un point de vue écologique, si l'on considère la possibilité que cette présence feuillue continue soit essentiellement causée par l'enfeuillement après coupe. Compte tenu que l'aménagement forestier extensif soit toujours le plus fréquent de tous les types d'aménagement (Benson 1988; Erdle et Ward 2008), une telle éventualité pourrait s'avérer une sérieuse menace à la productivité forestière résineuse et à l'aménagement forestier durable. Pour l'instant, cette importante question demeure sans réponse.

La prévision des impacts de la tordeuse

L'échantillonnage après une épidémie à l'échelle du peuplement est plus simple et généralement plus accessible, d'où l'abondance d'études à court terme sur les conséquences de l'aménagement dans un contexte de la TBE. Or, si l'objectif est d'effectuer une planification forestière qui considère les risques d'épidémies, des outils de modélisations sont nécessaires (Erdle et MacLean 1999). De même, les études terrain ne permettent pas de répondre aux questions concernant la dynamique à long terme de ces deux perturbations et de leurs interactions, d'où le manque de connaissance à ce chapitre (Miller et Rusnock 1993; Robert et al. 2012).

Différents rapports ont recommandé une meilleure intégration des dommages liés à la TBE dans la planification forestière, mais à ce jour, peu d'outils n'adressent explicitement cette question (Vérificateur général du Québec 2002; Duchesne and Raulier 2004; Couture et al. 2009). Considérant l'ampleur de ces pertes, ignorer la TBE dans les prévisions de productivité forestière augmente les risques de surestimation de la productivité et éventuellement peut mener vers une perte de capital forestier (Duchesne et Raulier 2004). Toutefois, un outil adressant cette question existe, le système d'aide à la décision (ForPRO), qui est actuellement utilisé au Nouveau-Brunswick pour établir des scénarios de sévérité d'épidémie et de pertes de volumes (MacLean et al. 2001; Hennigar et al. 2007). La défoliation par la TBE ne génère pas toujours une mortalité des hôtes, mais plutôt des pertes de croissance, généralement plus complexes à estimer sans l'aide d'un modèle de croissance par peuplement et d'un modèle d'approvisionnement forestier permettant d'extrapoler les résultats à grande échelle. Puisqu'il est difficile de prédire le moment du début, la durée et la sévérité d'une épidémie (Royama 1984), une approche par scénario est préférable dans la planification forestière (MacLean et al. 2000). La particularité d'une telle approche est sa capacité à évaluer un éventail de possibilités, améliorant ainsi la prise de décision (Schoemaker 1995), ce qui devient particulièrement utile sachant qu'une épidémie ne répète rarement le même patron que la précédente (Gray et al. 2000).

Ces dernières années, le progrès dans la modélisation de la dynamique forestière permet la simulation d'interactions complexes entre les perturbations forestières et la dynamique successionnelle à l'échelle du paysage (Mladenoff 2004). Plusieurs modèles de paysage forestier (e.g. SELES (Fall and Fall 2001), LANDIS-PRO (Wang et al. 2014) , LANDIS-II (Scheller et al. 2007), etc.) arrivent maintenant à gérer ce niveau élevé de complexité (Larocque et al. 2016). Ces modèles permettent d'adresser la problématique complexe des interactions entre l'aménagement et la TBE sur un horizon d'épidémies successives en fonction des conditions forestières environnantes. Ces questions impliquent de grandes échelles spatiales et temporelles et une approche de simulation basée uniquement sur des relations empiriques confine les projections dans la fenêtre restreinte des patrons observés par le passé (Porté et Bartelink 2002). Néanmoins les modèles de paysage forestier ne possèdent pas l'aspect pratique, la précision et la simplicité d'un modèle à l'échelle du peuplement comme ForPRO, d'où l'utilité complémentaire de ces deux approches afin de cerner la question de l'efficacité des mesures sylvicoles préventives contre la TBE.

Objectif général et plan de la thèse

Dans son ensemble, cette thèse cherche à évaluer l'efficacité de l'approche sylvicole préventive visant à réduire la sévérité des épidémies et les dommages liés à la TBE et ce, en passant de l'échelle du peuplement à l'échelle régionale et de l'échelle d'une épidémie unique à l'échelle d'épidémies successives. Cette efficacité étant potentiellement dépendante de la sévérité des épidémies successives, une importance particulière a été apportée à ce facteur. Le rendement en bois résineux constitue véritablement l'unité de référence commune dans chacun des chapitres de cette thèse. L'abondance et le rôle des feuillus y est particulièrement suivi, considérant qu'il agit à la fois positivement et négativement sur le rendement résineux en contexte de TBE.

Pour répondre à l'objectif général, la thèse a abordé trois sous-objectifs:

1) Puisque plusieurs modifications de la composition et de la structure sont survenues dans les dernières décennies et que les traitements sylvicoles préventifs appliqués depuis la dernière épidémie de TBE font partie de ces changements, le premier sous-objectif est d'évaluer l'efficacité de l'approche sylvicole préventive utilisée jusqu'à présent afin de réduire les dommages futurs causés par la TBE.

2) Considérant qu'il y a une augmentation de l'abondance des feuillus en sapinière aménagée et non-aménagée depuis la dernière épidémie de TBE et compte tenu de l'étendue de ce phénomène, les impacts méconnus de ce changement sur le couvert forestier et les rendements ligneux risquent d'avoir une grande importance économique. Le deuxième sous-objectif vise à caractériser le changement de composition à l'échelle du peuplement en lien avec la composition dominante dans le paysage et de déterminer les rôles de la TBE et des coupes dans ces changements de composition.

3) La planification forestière se fait sur les horizons de temps qui incluent de multiples perturbations agissant en parallèle ou successivement, produisant des interactions spatiales

et temporelles entre l'aménagement forestier et la TBE sur un horizon de plusieurs épidémies. Par conséquent, le troisième sous-objectif cherche à déterminer l'efficacité des stratégies d'aménagement préventif après plusieurs épidémies successives selon différents types de couvert initial et sévérité d'épidémie, ainsi qu'à évaluer l'effet des interactions entre ces deux perturbations sur la vulnérabilité des forêts.

CHAPITRE 1

ESTIMATING FOREST VULNERABILITY TO THE NEXT SPRUCE BUDWORM OUTBREAK: WILL PAST SILVICULTURAL EFFORTS PAY DIVIDENDS?

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1.1 ABSTRACT

Silvicultural treatments recommended to reduce damage by spruce budworm (SBW) (*Choristoneura fumiferana* [Clem.]) include reducing balsam fir (*Abies balsamea* (L.) Mill.) abundance and age, and increasing spruce (*Picea* spp.) and hardwood content. To evaluate the effect of these measures on forest timber supply, we assessed stand characteristics, disturbance history and timber supply for an intensively managed eastern Québec forest from 1985 to 2004, encompassing a major SBW outbreak. During this time, mean stand age declined from 55 to 51 years, and proportions of areas in balsam fir stands declined (42% to 27%), spruce-fir stabilized (12% and 11%), and mixedwoods increased (32% to 52%). We estimated forest vulnerability using softwood volume reductions following simulated outbreak scenarios of different severity (low, moderate and high) and effect of hardwood content in reducing fir-spruce defoliation. Volume reductions for outbreaks simulated to begin in either 1985 or 2004 were similar, ranging from 15-46% (no hardwood effect in reducing defoliation) to 13-39% (given a maximum hardwood content effect) for light and severe outbreaks. Considering the net detrimental effect of increased hardwood content on softwood timber supply, we question the dividends of promoting hardwoods and recommend increasing the combined use of plantations and weeding treatments to increase spruce content.

1.2 RÉSUMÉ

Les traitements sylvicoles recommandés pour réduire les dommages lors d'épidémies de la tordeuse des bourgeons de l'épinette (TBE) (*Choristoneura fumiferana* [Clem.]) incluent la réduction de l'abondance et de l'âge du sapin (*Abies balsamea* (L.) Mill.) et l'augmentation de l'abondance d'épinettes (*Picea* spp.) et de feuillus. Afin d'évaluer l'effet de ces mesures sur l'approvisionnement en bois, nous avons évalué de 1985 à 2004 les caractéristiques, l'historique des perturbations et l'approvisionnement en résineux d'une forêt de l'est du Québec sous aménagement intensif et pendant une épidémie majeure de TBE. Pendant cette période, l'âge moyen des peuplements a chuté de 55 à 51 ans, la proportion de peuplements de sapin a chuté (42% à 27%), celle d'épinette-sapin s'est maintenue (12% à 11%) et celle mixte a augmenté (32% à 52%). La vulnérabilité des forêts a été estimé à partir des réductions de volume résineux suivant des simulations d'épidémies de différentes sévérité (faible, modérée et sévère) et effet des feuillus sur la réduction de la défoliation des hôtes. Les pertes de bois des épidémies débutant en 1985 ou 2004 se sont avérées similaires et s'élevaient de 15-46% (aucun effet des feuillus) à 13-39% (effet des feuillus maximal) pour les épidémies légères et sévères. Étant donné la difficulté d'augmenter l'abondance d'épinettes et les pertes nettes de production résineuse liées au contenu élevé en feuillus, nous remettons en question les bénéfices liés à la préservation des feuillus et recommandons une utilisation accrue du contrôle de la végétation en plantation pour augmenter l'abondance d'épinette.

1.3 INTRODUCTION

The last spruce budworm (*Choristoneura fumiferana* [Clem.]; SBW) outbreak, which occurred from 1967 to 1992 in eastern Canada and the U.S., generated an estimated annual loss of 44×10^6 m^3 of timber volume at the peak of the outbreak, from 1977 to 1981 (Power 1991). Several studies have examined forest management treatments that could help prevent or reduce losses to future SBW outbreaks (Baskerville 1975b; Blum and MacLean 1984; MacLean 1996). Evidence suggests that silvicultural treatments and forest management planning can reduce forest vulnerability either through stand age reduction, species composition manipulations or prioritized harvesting of the most susceptible stands (MacLean 1996). Forest susceptibility is defined here as the probability of a forest being defoliated by the SBW and forest vulnerability as the probability of growth reduction and mortality resulting from defoliation (MacLean and MacKinnon 1997). The logic of silvicultural manipulations to reduce vulnerability is to decrease abundance of mature (> 40 yrs) balsam fir- (*Abies balsamea* (L.) Mill.) dominated stands (MacLean 1980), in favor of younger and less vulnerable spruce species. Yet, the impact of silvicultural manipulations to reduce SBW impacts on stand dynamics and softwood timber supply has not been assessed.

The effect of species composition on forest vulnerability to the SBW led to the emergence of the silvicultural hypothesis, which posits that past forest management has increased SBW outbreak severity by increasing balsam fir abundance and that appropriate management can reduce fir abundance and consequently, the damage caused by the SBW (Blais 1983; Miller and Rusnock 1993). Despite being contested on the basis of missing detailed historical data and lack of manipulative studies (Miller and Rusnock 1993; Koricheva et al. 2006, but see Robert et al. 2012), this hypothesis has been operationally implemented, often to a great extent and with large investments (Gagnon and Chabot 1991; Chabot et al. 2013). The main prophylactic treatments against SBW are replacement of natural balsam fir with spruce plantations (Hennigar and MacLean 2010), precommercial thinning (PCT) to increase spruce content and reduce competing vegetation (Pothier 2002; Pothier et al. 2012), and promotion of hardwood content (Chabot et al. 2013). In recent decades, large scale forest management has considerably modified forest cover in parts of the SBW-susceptible forest, reducing average stand age and altering tree species composition (Blais 1983; Belle-Isle and Kneeshaw 2007; Cyr et al. 2009), characteristics that essentially determine stand vulnerability to SBW outbreaks (MacLean 1980; Erdle and MacLean 1999).

In addition to forest management, the severe 1967-1992 SBW outbreak caused extensive tree mortality and stand renewal (Blais 1983). The most vulnerable mature stands composed of balsam fir and white spruce (*Picea glauca* (Moench) Voss) are now less abundant, younger, and thus less vulnerable to the SBW than at the time of the last outbreak (Bouchard et al. 2006). A large amount of SBW-killed or timber harvested stands also regenerated with a higher proportion of non-host species such as paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Bouchard et al. 2006; Spence and MacLean 2012). Evidence suggests that these and other hardwood species could reduce defoliation and susceptibility to the SBW, either due to the increased diversity of the SBW's natural enemies or to dispersal barriers generated by non-host tree species (Su et al. 1996; Cappuccino et al. 1999; Campbell et al. 2008).

Severe SBW outbreaks as well as forest management also generate younger and consequently less vulnerable forest cover (MacLean 1988; Etheridge et al. 2005; Bouchard et al. 2007). Severe SBW outbreaks cause partial mortality in immature cohorts (Ruel and Huot 1993; MacLean and Andersen 2008), which increases the time necessary for mature balsam fir-dominated forest cover to re-establish after the outbreak, thereby reducing forest vulnerability for intervals of 50 years or more (Blais 1981; Erdle and MacLean 1999; Bouchard et al. 2006). It has been reported that the three previous SBW outbreaks in Québec followed such a cyclical pattern, with the 1909-1920 outbreak being severe, the 1938-1958 outbreak less severe than its predecessor, and the 1967-1992 outbreak severe (Bouchard et al. 2006; Bouchard et al. 2007). This natural cycle along with the impression of having created forests of lower vulnerability due to preventive silviculture has led to the expectation that the next SBW outbreak will be less severe than the 1967-1992 outbreak

(Coulombe et al. 2004; Morin et al. 2007; James W. Sewall Company 2011), but this assertion remains to be tested.

From 1973 to 1992, a severe SBW outbreak occurred in the Gaspé region in eastern Québec, Canada, and caused tree mortality across 47% of the area. Objectives of this study were to: (1) determine how forest species composition and age have changed since the last SBW outbreak in a severely impacted forest; (2) simulate effects of SBW outbreak scenarios, with and without hardwood reduction of defoliation, on volume reduction during the last outbreak and under current forest conditions; and (3) estimate effectiveness of preventive forest management measures (plantation, PCT, and hardwood retention) in modifying forest composition and age and consequently, decreasing volume reductions under SBW outbreak scenarios.

1.4 METHODS

1.4.1 Study area

The 104 000 ha Gaspé management unit study area is comprised of natural forests dominated by balsam fir in mixes with hardwoods (Fig. 1.1). SBW host species present in the area, in decreasing order of susceptibility (Hennigar et al. 2008), are balsam fir, white spruce, red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* [Mill.] B.S.P.). Hardwood species were, from the most to the least abundant, white birch, trembling aspen (*Populus tremuloides* Michx.), maple (*Acer* spp.), pin cherry (*Prunus pensylvanica* L. f.), and yellow birch (*Betula alleghaniensis* Britt.). Non-host conifers such as eastern white cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), and jack pine (*Pinus banksiana* Lamb.) accounted for less than 1% of the total volume.

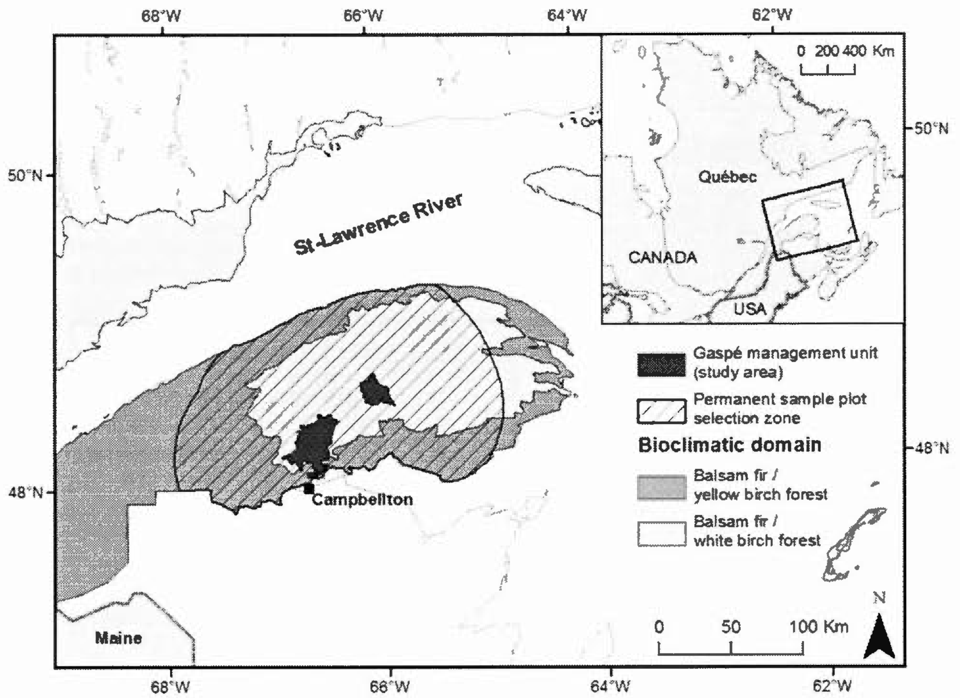

Figure 1.1. Map of the Gaspé Peninsula and study area (separated into two bioclimatic zones).

The use of intensive forest management in the study area was relatively high with 15% of the area treated with PCT by 2004, and 7% of the study area in plantations, mostly black and white spruce (white (42%), black (31%) and Norway spruce (*Picea abies* (L.) Karsten) (12%), jack pine and tamarack (6%), and unknown species (9%)) according to the SIFORT database "Système d'Information FORestière par Tesselle", a large scale, 14 ha-resolution systematic sampling grid based on stand information (Pelletier et al. 2007). A total of 80% of the study area was disturbed from 1958 to 2004 by either SBW, harvesting (mostly clearcutting, see below) or intensive management (plantation and/or PCT); other disturbances affected < 1% of the study area.

1.4.2 Forest inventory data

Stand characteristics in the Gaspé management unit were determined using 7399 sample points from the SIFORT database, a large scale systematic sampling grid with a 14 ha resolution, based on stand information interpreted from aerial photos (Pelletier et al. 2007). Forest species composition and age per sample point was determined from successive inventories in 1985-1986, 1992-1993, and 2004 (hereafter referred to as the 1985, 1992, and 2004 inventories). A previous inventory (1974), conducted prior to the start of the 1973-1992 SBW outbreak (the first large scale inventory undertaken in Quebec) was also initially included in our analysis, but was removed due to stand age-related inconsistencies. In addition to having only 3 different stand age classes (10, 30, 90), the 1974 inventory for the study area had 20% of stands reporting a stand age > 2 age classes younger (>21 years) than in the 1985 inventory (11-year interval) (vs. 8% in 1992, and 5% in 2004).

Inventory-derived data on forest composition and stand age change for the same period were compared to the Québec Ministry of Natural Resources (QMNR) permanent sample plot (PSP) database. PSPs were measured in 1974-77, 1981-86, 1995-97, and 2003-2005 (hereafter referred to as 1974, 1981, 1995, and 2003), which covers the 1973-1992 SBW outbreak period in the region. The PSP network in Québec is not subject to protection from forest management, which makes its disturbance history similar to that of the study area. A total of 219 plots were selected either within or up to 75 km outside but within the same bioclimatic domains forest types as in the study area (Fig. 1.1).

The dominant stand age, forest cover composition, initial disturbance (severe SBW outbreak, wildfire, or clearcut + plantation) and partial disturbance (light/moderate SBW outbreak, wildfire, PCT or partial cut) were recorded for each stand in the SIFORT database within the study area. Sampling methods were generally similar between inventories, with minor inconsistencies regarding stand composition and uneven-aged stands. We summarized stand composition data into three stand types: balsam fir stands (> 75% in basal area), spruce-fir stands (spruce ≥ 50%, balsam fir < 50%), and mixedwood stands (hardwoods ≥ 25%). Categories of young and old uneven-aged stands based on the estimated age of the oldest stems, differed between 1985 (< 60 years versus > 60 years) and 2004 (< 80 years versus > 80 years inventories). For simulation purposes, the ages of young and old uneven-aged stands were assumed to be 40 and 80 years old in 1985 and 50 and 90 years old in 2004. In all cases, uneven-aged stands were thus considered to be mature (> 40 years) with regards to SBW, which reduced the consequences of this inconsistency in our analyses.

1.4.3 Simulation of SBW outbreak scenarios

We used the Accuair ForPRO system (Forus Research 2010; McLeod et al. 2012), commonly known as the Spruce Budworm Decision Support System (SBWDSS), to analyse stand vulnerability to the SBW. This tool is made up of four components: (1) a defoliation/ damage database (Erdle and MacLean 1999); (2) an estimated volume reduction database as a function of cumulative defoliation and stand type (i.e. the Stand Impact Matrix (SIMPACT)) (MacLean et al. 2001); (3) a timber supply model (in our case the Remsoft Spatial Planning Framework) (Remsoft Inc. 2008); and (4) the ForPRO system to link the previous three components. Timber yields were estimated using the Quebec PSP network and the ARTEMIS-2009 tree-level growth model (Fortin and Langevin 2010). Because the Remsoft Spatial Planning Framework has a deterministic framework (no form of uncertainty is integrated), ForPRO is usually used in a scenario planning approach, with a range of optimistic to pessimistic future scenarios (MacLean et al. 2001). Scenarios help overcome the absence of uncertainty in deterministic models as long as a plausible range of possibilities is used (Schoemaker 1995).

Simulations of effects of light, moderate, and severe SBW outbreak scenarios (Fig. 1.2) on potential timber volume were initialized using SIFORT forest inventory characteristics in 1985 and 2004. The resulting peak SBW outbreak-caused timber volume reductions (after 10 years for the light outbreak scenario and after 15 years for moderate and severe outbreak scenarios) were compared to determine how forest vulnerability to SBW changed over this period. With average intervals between SBW outbreaks of approximately 30 years (Bouchard et al. 2006; Robert et al. 2012), a SBW outbreak could possibly occur in 2004 (31 years after the start of the 1973-1992 outbreak. However, our objective was to use ForPRO simulations of the 1985 and 2004 forest conditions as a measure of effectiveness of forest management actions in reducing vulnerability.

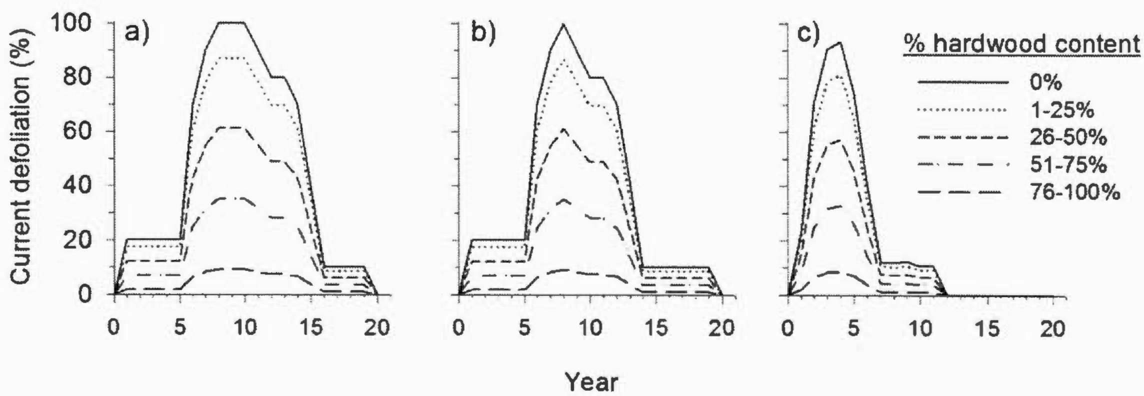

Figure 1.2. Hardwood content effect on balsam fir defoliation due to spruce budworm given: (a) severe (MacLean et al. 2001), (b) moderate (MacLean et al. 2001), or (c) light (modified from Gray et al. 2000) outbreaks. Hardwood effects were assumed to be constant throughout the outbreak and directly proportional to stand hardwood content, based on Su et al. (1996).

The three SBW outbreak severity scenarios simulated (Fig. 1.2a-c) were: 1) a light outbreak present in the Gaspé region during the 1973-1992 SBW outbreak (Gray et al. 2000), characterized by 5 years of moderate defoliation (30-70%) and 1 year of severe defoliation (>70%); 2) a moderate outbreak including 3 years of moderate and 5 years of severe defoliation (MacLean et al. 2001); and 3) a severe outbreak including 3 years of moderate and 7 years of severe defoliation (MacLean et al. 2001). Outbreak duration varies considerably within outbreaks; the last SBW outbreaks lasted more than 20 years in some places and much less in others (Gray et al. 2000). The 10-year maximal duration simulated here is a typical outbreak duration at a given site, but because ForPRO uses cumulative defoliation values, 6 additional years of defoliation are also considered in the simulated outbreak duration. Nevertheless, specific outbreak duration was not fundamental here as we did a comparative analysis across three outbreak severities/durations, forest conditions and management scenarios. Unlike MacLean et al.'s balsam fir defoliation estimates, Gray et al. (2000) used aerial defoliation estimates, meaning defoliation is averaged over the stand and potentially underestimates balsam fir defoliation in all stand types except pure balsam fir stands. Furthermore, they used class midpoints and likely underestimated maximum annual defoliation by about 20% (Campbell 2008). We therefore modified the light outbreak scenario by increasing annual defoliation values by 20% during outbreak rise and by 10% during outbreak decline (MacLean et al. 2001), to account for build-up of natural enemy populations as the outbreak progresses (Royama 1992). Collectively, the three SBW outbreak patterns define a plausible range of defoliation severity. Given that most trees sampled for monitoring SBW populations were balsam fir, outbreak scenarios primarily represent defoliation trends on fir. Based on Hennigar et al. (2008), defoliation on white, red, and black spruce was recalculated throughout the outbreak as 72%, 41%, and 28% of that on balsam fir. Average 5-year cumulative defoliation per SBW outbreak scenario by hardwood content class and 5-year periods is presented in Table 1.1.

Tableau 1.1 Average cumulative balsam fir defoliation (%) for the severe, moderate, and light spruce budworm outbreak scenarios as a function of stand hardwood content, based on relationships from Su et al. (1996).

Outbreak scenario	Hardwood content class (%) [a]	Average periodic cumulative defoliation (%) [b]	
		Period 1	Period 2
Severe	Pure SW	67	85
	SW-dominated	59	74
	SW-HW	41	52
	HW-dominated	24	30
	Pure HW	6	8
Moderate	Pure SW	65	63
	SW-dominated	59	55
	SW-HW	40	38
	HW-dominated	23	22
	Pure HW	6	6
Light	Pure SW	45	39
	SW-dominated	39	34
	SW-HW	28	24
	HW-dominated	16	14
	Pure HW	4	4

[a] Hardwood (HW) content classes, in percent of total stand volume: pure softwood (SW) (0% hardwood), softwood-dominated (1-25%), softwood-hardwood (26-50%), hardwood-softwood (51-75%), and hardwood-dominated (> 75%).

[b] Outbreak patterns in Fig. 1.2 were converted into two 5-year simulation periods corresponding to years 6-10 and 11-15 (severe and moderate outbreaks) and years 1-5 and 6-10 (light outbreak).

Because hardwood content has been identified as reducing stand level vulnerability to SBW, we tested effects of incorporating defoliation reductions related to stand hardwood content based on averaged balsam fir defoliation in a 3-year period before outbreak decline in New Brunswick from Su et al. (1996). Given the common belief that natural enemies have a relatively constant impact throughout outbreak duration at many spatial scales (Cappuccino et al. 1998; Campbell et al. 2008), we assumed a constant hardwood content effect reducing spruce-fir defoliation throughout the outbreak (Fig. 1.2a-c).

Since all spruce species were combined within our set of yield curves and because there are substantial, known differences in vulnerability between spruce species, we had to consider them as either one of the two most abundant spruce species in the Gaspé region, i.e. white or black spruce. In determining the effectiveness of intensive management (objective 3), we simulated SBW impacts using black spruce and white spruce alternatively (see below). In evaluating the comparative impacts of SBW outbreaks on the 1985 and 2004 forest composition (objective 2), the choice of spruce species was of minor importance since we looked at relative, not absolute SBW damage. For the latter objective, we thus chose black spruce as the default spruce species for the simple reason that it was more abundant than white spruce in the Gaspé region (51-59% of merchantable spruce stems in the PSPs vs. 48%-32% for white spruce, 1-3% for red spruce, and 0-6% for Norway spruce in 1974 and 2003, respectively). White spruce being usually more productive than black spruce, we expect our combined spruce yield to slightly underestimate and overestimate white and black spruce yield, respectively.

1.4.4 Silvicultural treatments description, impact evaluation and assumptions

We compared effectiveness of silvicultural treatments in decreasing volume reductions following a SBW outbreak and in increasing post-outbreak softwood yield. Some of the harvesting was done with partial cutting (undistinguished treatments: likely diameter-limit cutting or salvage logging (M. Huot, personal communication); 20% of harvested area), but most was clearcutting (80% of harvested area). All treatments were post-harvesting, but were grouped into extensive management (harvesting only, natural regeneration), or preventive/intensive management: precommercial thinning (PCT; mechanical thinning of competing vegetation), plantation (black/white spruce, no subsequent thinning), and cleaned plantation (combined use of plantation and PCT).

About 20% of managed stands were also affected by SBW mortality, but the SIFORT inventory likely underestimated their abundance as it records only one disturbance (major and/or minor disturbance) per measurement year. There was no difference in the 1985-2004 composition change between managed-only stands and stands affected by both SBW and management, and therefore we grouped all managed stands, whether also affected by SBW or not.

We evaluated the effect of silvicultural treatments from 1985 to 2004 on species composition in 2004 by selecting stands that were balsam fir stand type in 1985. The resulting forest composition for each treatment type was then used to assess the effectiveness of past forest management in decreasing volume reductions and in increasing softwood yields following a severe SBW outbreak scenario (10-year duration, including the hardwood content effect) for mature, 70-year old stands. We grouped silvicultural treatments in terms of their impact on forest composition: increased mixedwoods, increased spruce, balanced composition, and unmanaged. Silvicultural treatments were also evaluated with regards to the spruce species used, whose vulnerability to SBW vary substantially. We thus conducted and compared two simulations in which spruce volume was either exclusively composed of white spruce, a preferred host, or black spruce, a minor host.

1.5 RESULTS

1.5.1 Change in forest composition and age from 1985 to 2004

In 1985, the 103,600-ha study area had 43,600 ha of balsam fir stands (the most vulnerable stand type to SBW outbreaks; 48% of the study area with known composition), 33,400 ha of mixedwood (37%), 13,800 ha of spruce-fir stands (15%), and 12,800 ha with unknown composition. By 2004, balsam fir had decreased by 26,000 ha to 17,600 ha (20% of the study area with known composition), mixedwoods increased by 20,600 ha to 54,000 ha (63%), and spruce-fir increased by 1,300 ha to 15,100 ha (17%).

Changes in stand type in the Gaspé region (see Fig. 1.1 for area delimitation) during the 1981-2003 period based on PSP data showed similar (albeit slightly smaller) patterns to the stand level data for the 1985-2004 period: balsam fir abundance decreased from 42%-33% in the plots vs. 48%-29% of stands, spruce-fir increased from 12%-17% in the plots vs. 15%-16% of stands, and mixedwood increased from 46%-50% in the plots vs. 37%-56% of stands (Fig. 1.3). The stand type change in PSPs from 1974-1981 (during the initial phase of the 1973-1992 SBW outbreak) was substantial: a 9% decrease for balsam fir plots, with a corresponding increase of 1% for spruce-fir plots, and 8% for mixedwood plots. The balsam fir/mixedwood proportion thus decreased throughout the 1974-1995 period, but the trend was inverted for the 1995-2003 period, i.e. after the 1973-1992 SBW outbreak as balsam fir increased by 3% and mixedwoods decreased by 5%.

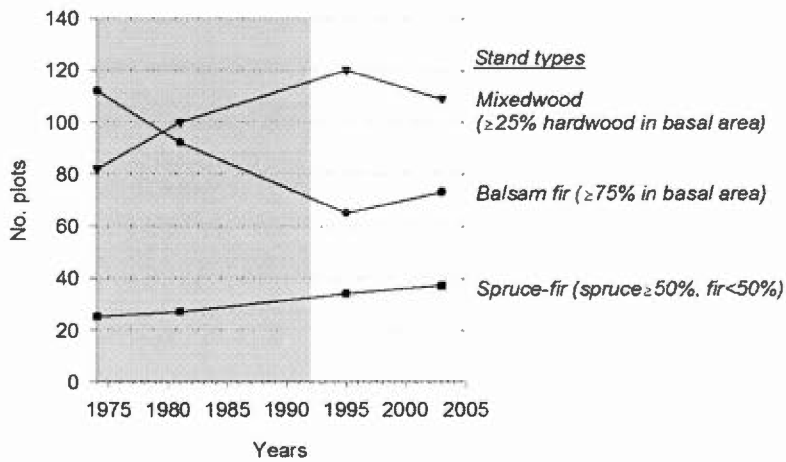

Figure 1.3. Species composition of 219 permanent sample plots located within a 75 km radius of the study area by stand type from 1974 to 2003. Years in grey represent the spruce budworm outbreak period (1973-1992).

These trends were also present with softwood volume in the study area, but in that case balsam fir stands still remained the dominant source of softwood timber by 2004, with 50% of total softwood yield relative to 63% in 1985. The fact that balsam fir stands had the highest softwood yield of all stand types is responsible for this disparity relative to area proportion changes.

Overall, balsam fir stand age structure remained similar between 1985 and 2004, with a dominance of mature, 41-60 years and 61-80 years age classes, while other stands (mixedwood and spruce-fir stands) age structure went from a relatively uniform distribution to an inversed-J structure dominated by young stands (Fig. 1.4a-b). The similarity in balsam fir age structure between 1985 and 2004, along with composition changes shown in Fig. 1.3, suggest that balsam fir stands affected by SBW switched to the "other stand" composition type, hence the pronounced inversed-J structure in the latter stand type. In terms of stand maturity, the extent of mature (> 40 years) balsam fir stands, more vulnerable than immature (≤ 40 years) stands to SBW outbreaks, remained similar at 77% and 78% of total fir stands, (Fig. 1.4c-d). In comparison, other stand types had a fewer mature stands, at 63% mature in 1985 and 58% in 2004.

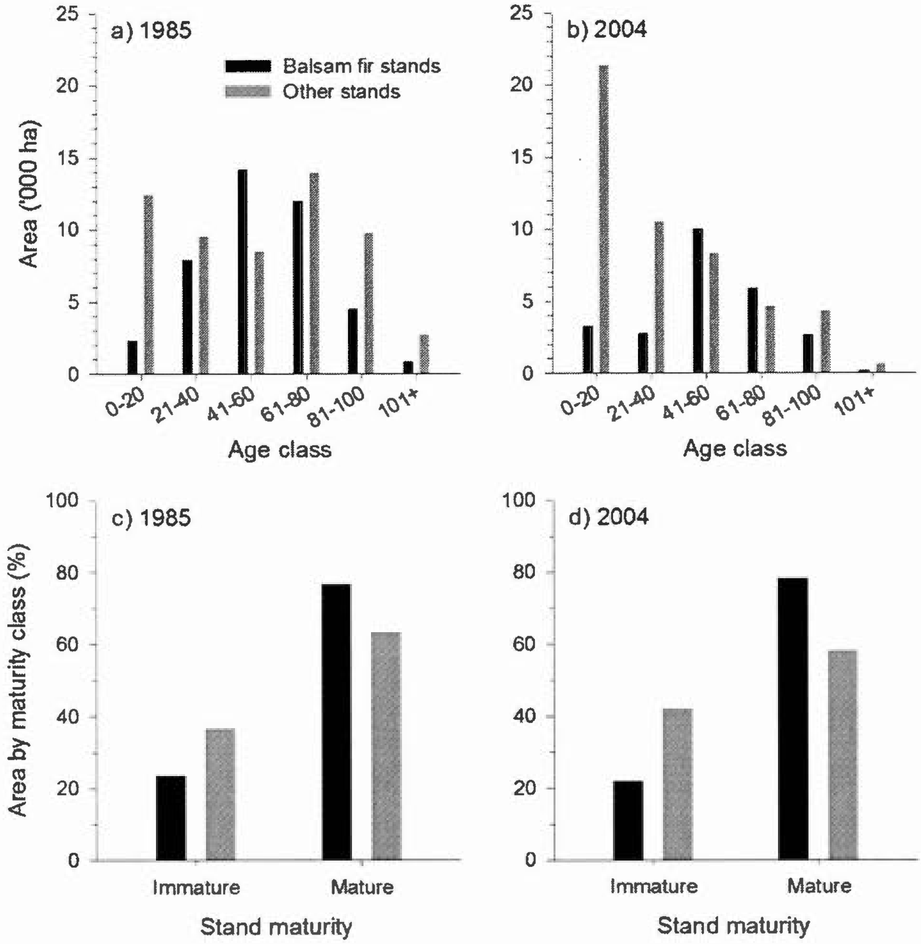

Figure 1.4. Age class distribution (a-b) by area and percentage of area by maturity class (c-d) (immature: ≤40 years; mature: >41 years) for balsam fir stands and other stands (mixedwood and spruce-fir) in the study area in 1985 and 2004. Uneven-aged stands, rare in 1985 (<5% of study area), but more frequent in 2004 (35% of balsam fir stands, 11% of other stands), were excluded from a-b, but included in the simulations and c-d as mature stands (see Methods).

1.5.2 Simulation of SBW outbreaks effect on volume yields – no hardwood content effects

Actual softwood volume in the study area decreased from 7.5 Mm^3 to 6.5 Mm^3 between 1985 and 2004 (starting point of simulations in Fig. 1.5). This initial difference increased during the 15-year simulation period due to higher average softwood productivity (i.e., slope of the undefoliated lines in Fig. 1.5) in the undefoliated 1985 simulation (77,500 m^3/year) than in the 2004 simulation (47,500 m^3/year). This was essentially due to the older age of spruce-fir and mixedwood stands in 1985 relative to 2004, and the fact that balsam fir stands, which had the highest softwood yield among all stand types in 2004 (balsam fir: 118 m^3/ha; spruce fir: 77 m^3/ha; mixedwood: 38 m^3/ha), had declined relative to 1985.

Softwood volume yield for the undefoliated scenario was of 8.7 Mm^3 and 7.3 Mm^3 at the end of the 1985 and 2004 simulations, respectively. Total volume reductions caused by SBW outbreak scenarios (with no hardwood content effect on spruce-fir defoliation) for the study area (i.e., undefoliated scenario volume minus the minimum yield, black dots in Fig. 1.5) were higher in the 1985 than the 2004 simulations: 1.2 and 1.0 Mm^3 for the light outbreak, 2.9 and 2.4 Mm^3 for the moderate outbreaks and, 3.9 and 3.3 Mm^3 and for the severe outbreak scenarios (Fig. 1.5). However, in terms of percentage volume reduction, the difference between the 1985 and 2004 simulations (no hardwoods effect scenario) was almost nil, with 15 vs. 15%, 33 vs. 34%, and 45 vs. 46% and volume reductions for 1985 and 2004 simulations during light, moderate, and severe outbreak scenarios, respectively.

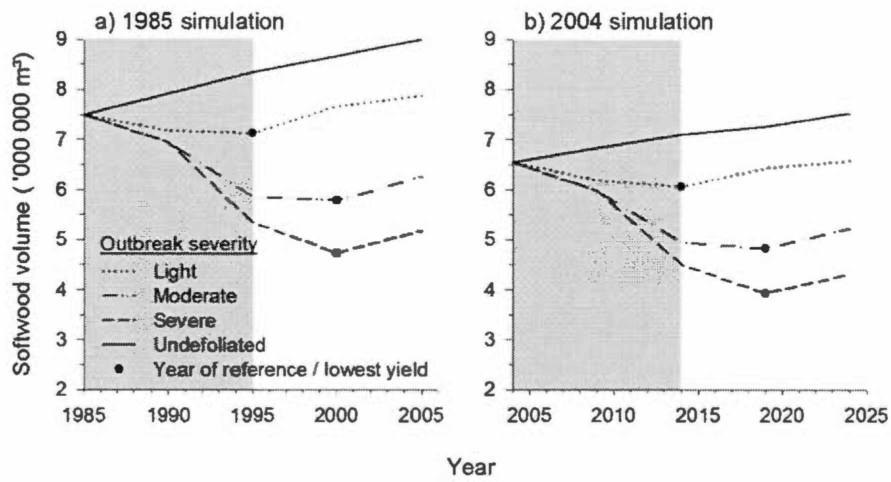

Figure 1.5. Softwood volume yield for 20-year simulations initiated using a) 1985 and b) 2004 Gaspé management unit forest conditions, under undefoliated and three spruce budworm outbreak severities with no hardwood content effect on defoliation. The 10-year duration spruce budworm outbreak period is shaded. Spruce yield (planted and natural regeneration) is composed of black spruce only (see Methods). Black dots represent the year of lowest yield, when SBW-caused volume reduction was calculated.

1.5.3 Simulation of SBW outbreaks effect on volume yields –hardwood content effects

The difference in percentage volume reduction between the 1985 and 2004 simulations were higher but still low when including the hardwood content effect to reduce spruce-fir defoliation at 14 vs. 13%, 30 vs. 29%, and 41 vs. 39% volume reductions for the light, moderate, and severe outbreak scenarios, respectively. Because these differences in percentage volume reduction were insignificant, we chose hereon to present only one of the two periods, the 2004 simulation, to simplify the presentation.

Simulated volume reductions, with and without hardwood content effects on reducing spruce-fir defoliation, were 13 and 15%, 29 and 34%, and 39 and 46% of undefoliated softwood yield volume reductions for light, moderate, and severe outbreak scenarios, respectively (Fig. 1.6).Total softwood volume "saved" by the protective effect of hardwoods increased with outbreak severity, totaling 11%, 13%, and 16%, of the maximal losses (i.e., in the no hardwood content effect) for light, moderate, and severe outbreak scenarios, respectively.

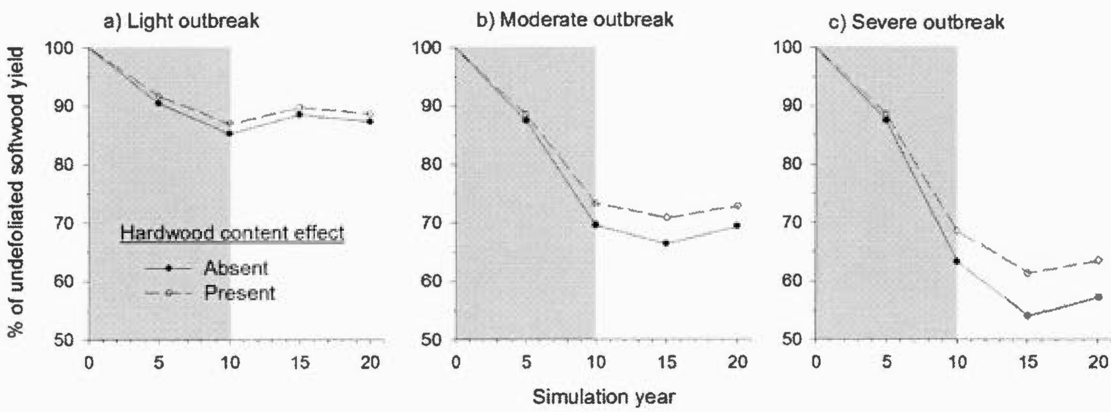

Figure 1.6. Softwood volume reductions (%) for simulations starting in 2004 given a) severe, b) moderate, and c) light spruce budworm outbreak scenarios (10-year duration outbreak; shaded area) with and without hardwood content effect reducing spruce-fir defoliation. Hardwood effects were assumed constant throughout the outbreak and directly proportional to stand hardwood content, based on Su et al. (1996).

The hardwood content effect substantially reduced mixedwood stand losses relative to the no hardwood content effect 2004 simulations, with 9% vs. 12%, 22% vs. 35%, and 25% vs. 47% volume reductions for simulations with and without hardwood content effect during, light moderate, and severe outbreak scenarios, respectively (Fig. 1.7). Black spruce-fir stands were generally the least affected stand type, with < 2% difference in volume reductions compared to mixedwoods (Fig. 1.7). Balsam fir stands, which had the highest volume reductions in all scenarios, had little difference between the simulations with and without hardwood content effect (<1% difference in volume reduction), with 16%, 38%, and 52% volume reductions including the hardwood content effect in light, moderate, and severe outbreaks, respectively. When using white spruce as the default spruce species during a severe outbreak scenario including the hardwood content effect, mixedwood stands were the least affected stand type with 30% volume reduction, followed by white spruce-fir stands with 41% volume reduction, and lastly balsam fir with 58% volume reduction (data not shown).In 1985, balsam fir stands accounted for 63% of total softwood volume and despite that their abundance had decreased by 2004, they still accounted for a majority of total softwood volume in the study area at 50%, mostly due to the increase in mixedwood stand abundance and their lower softwood yield. This partly explains why the volume reduction level stagnated between 1985 and 2004 in the study area. We did not find an improved softwood volume by 2004 either. With a maximum "saved" softwood volume of 0.53 Mm^3 simulated during a severe outbreak scenario including the hardwood content effect, the protective effect of hardwoods did not maintain sufficient softwood volume to offset the reductions associated with the softwoods being replaced by hardwoods, i.e. 1.4 Mm^3 from 1985 to 2004.

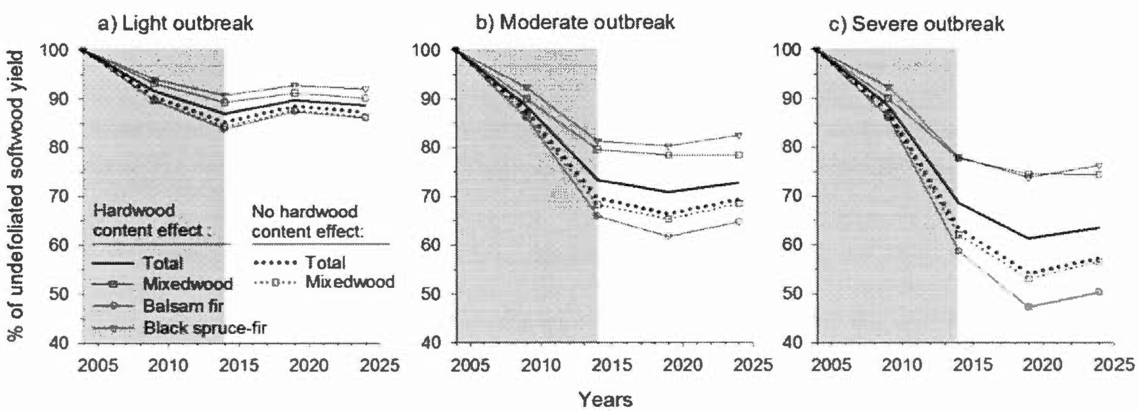

Figure 1.7. Softwood volume reductions (%) per stand type for simulations starting in 2004 with and without hardwood content effect in reducing spruce-fir defoliation. Three spruce budworm outbreak scenarios were simulated: a) severe, b) moderate, and c) light (10-year duration outbreak; shaded area). Spruce yield (planted and natural regeneration) was assumed to be composed of black spruce only (see Methods).

1.5.4 Effectiveness of silviculture in changing forest composition and limiting volume reductions following a SBW outbreak

From 1985 to 2004, 33,900 ha of the study area were undisturbed whereas the remainder was disturbed by SBW, intensive management, extensive management, or a combination of SBW and forest management. Specifically, 30,300 ha were affected by SBW only, 20,000 ha by intensive management (12,200 ha PCT, 4,500 ha plantation, and 3,300 ha of cleaned plantations), and 19,400 ha by extensive management. A proportion of managed stands were also affected by SBW, but as explained in the Methods, we grouped all managed stands, whether also affected by SBW or not, based on the limited influence of SBW on the 1985-2004 composition change within managed stands.

Balsam fir stands in 1985 composed 42% of the study area, and by 2004, there were substantial species composition changes depending upon the type of disturbance (Fig. 1.8). Only 39% of spruce plantations (uncleaned, i.e. without PCT) were still classified as having a spruce-fir composition while the others became either dominated by a hardwood-conifer mix (43%) or by balsam fir (18%) (Fig. 1.8). PCT stands (precommercial thinning; where competing vegetation was mechanically removed) were slightly better than uncleaned plantations in limiting hardwood encroachment as 33% of PCT stands had mixedwood composition by 2004. With 17% spruce-fir stands by 2004, PCT moderately increased the proportion of spruce-fir stands relative to extensive management and unmanaged stands, which had 1% and 15% spruce-fir stands by 2004, respectively. In contrast, cleaned plantations (i.e. combined with PCT) were the most effective of the evaluated silvicultural treatments in maintaining spruce-fir composition with 98% of treated stands being dominated by spruce-fir in 2004.

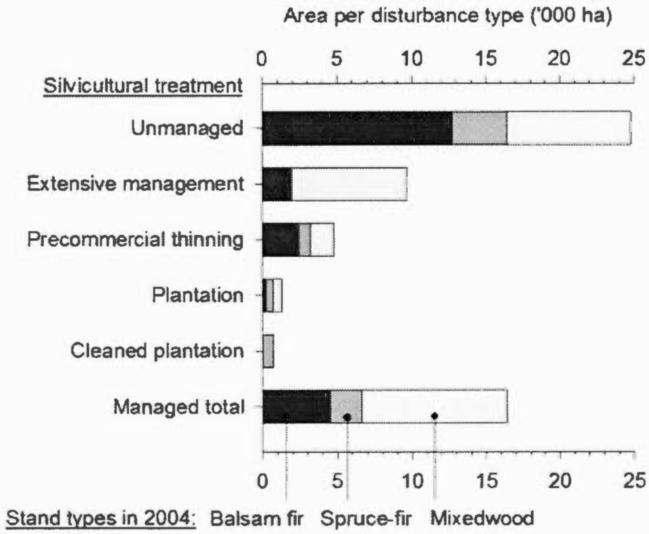

Figure 1.8. Effect of silvicultural treatment from 1985-2004 on species composition in 2004 of stands that were balsam fir stand type in 1985 (42% of the study area). Stands unmanaged between 1985-2004 were either undisturbed or affected by spruce budworm only. Extensive management excludes intensive treatments such as precommercial thinning, plantation, or both (cleaned plantation).

Overall, intensive management did not succeed in limiting competing vegetation, as 34% of PCT stands became mixedwoods and 62% of uncleaned plantations became either balsam fir or mixedwood stands, and a total of 29% of treated stands were spruce-fir stands by 2004. Hardwood encroachment was greatest on extensively managed sites, with 80% of treated stands having a mixedwood (hardwood-softwood) composition by 2004 (Fig. 1.8). However, stands unmanaged between 1985 and 2004 still experienced substantial hardwood encroachment, with 34% of stands having a mixed hardwood-softwood composition by 2004 (51% balsam fir, 15% spruce-fir).

Based on the effect of silvicultural treatment on forest composition presented in Fig. 1.8, we evaluated volume reduction and softwood yield 15 years after a severe SBW outbreak simulation (10-year duration) applied to 70-year old stands (Fig. 1.9). Four silvicultural /management regime effects were simulated: increased mixedwoods (from extensive management); increased spruce (from cleaned plantation); balanced composition (from plantation or PCT); and unmanaged stands. By the end of the outbreak simulation, treatments in black spruce-based simulations had lower volume reductions than in white spruce-based simulations, with averages of 43 and 51% volume reductions, respectively (Fig. 1.9a-b). Volume reduction was least under the increased spruce objective, assuming black spruce, at 20% by the end of the outbreak simulation (Fig. 1.9a), versus 38% assuming that spruce was white spruce (Fig. 1.9b). In comparison, volume reductions for unmanaged stands, increased mixedwood and balanced composition objectives were 43-44% assuming that spruce was black, versus 50-53% assuming that spruce was white.

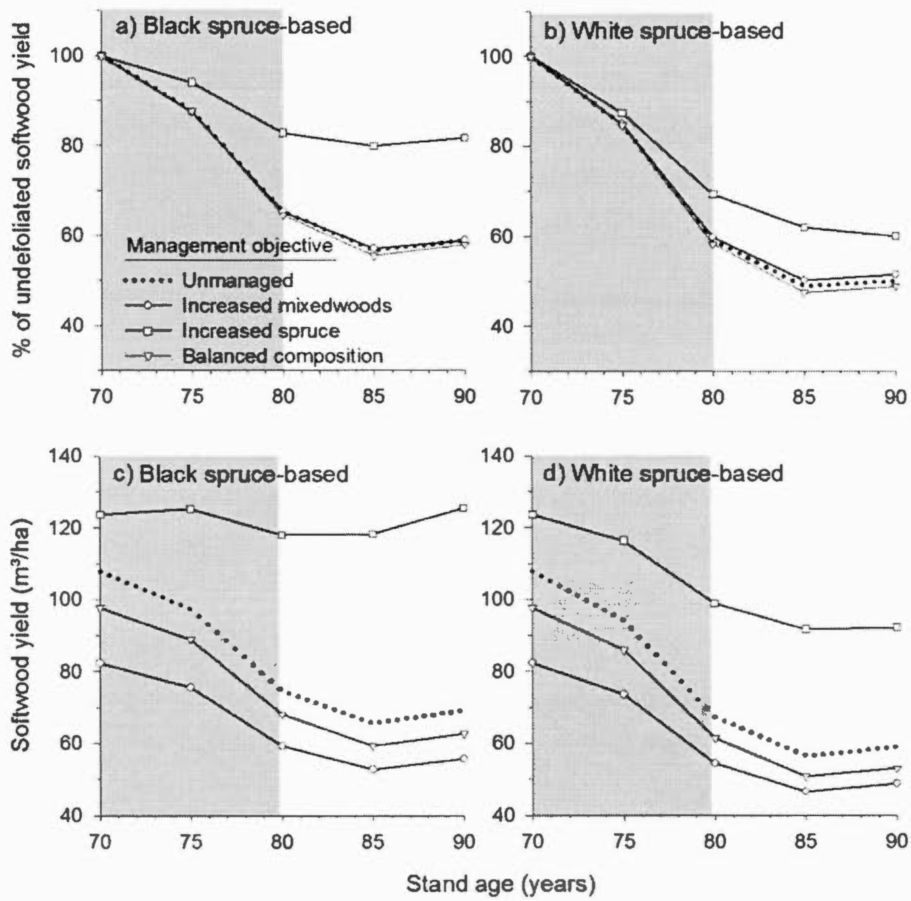

Figure 1.9. Volume reduction (a-b) and softwood yield (c-d) simulated for 70-year old stands representing different past silvicultural treatments during a severe spruce budworm outbreak scenario (including the hardwood content effect, 10-year duration; shaded area). Silvicultural treatments are as presented in Fig. 1.8: increased mixedwoods = extensive management; increased spruce = cleaned plantation; balanced composition = precommercial thinning or plantation; and unmanaged stands. Simulations consider all spruce as black spruce (a, c) or as white spruce (b, d).

Before the outbreak simulation, softwood yield of 70-year old stands was highest under the increased spruce management regime at 124 m^3/ha (Fig. 1.9 c-d). Due to a lower softwood and spruce content, the balanced composition (plantation or PCT) management regime had substantially lower softwood yields at 98 m^3/ha, than both increased spruce management and unmanaged stands at 108 m^3/ha. The increased mixedwood management regime yielded the lowest volume with 82 m^3/ha before the outbreak simulation. Post-outbreak softwood yields were higher assuming black spruce-based management regime simulations than white spruce-based simulations, with averages of 62 and 54 m^3/ha by the end of the outbreak simulation, respectively. Yet in both cases, the increased spruce (black or white) management had the highest post-outbreak softwood yield, at 118 and 92 m^3/ha, compared to 59 and 51 m^3/ha post-outbreak yield for the balanced composition management and 53 and 46 m^3/ha for increased mixedwood management simulations (Fig. 1.9c-d).

1.6 DISCUSSION

1.6.1 Variability of host resource abundance and vulnerability

It has been suggested that over a large spatial scale, an increase in hardwood content, reduction in large balsam fir accumulation, and younger stand age following severe SBW outbreaks and forest management could reduce forest vulnerability to the following SBW outbreak (Bouchard et al. 2007). We found substantial reductions in balsam fir and increases in hardwood content, and observed reductions in stand age, especially for mixedwood and spruce-fir stand types, which would reduce forest vulnerability to the SBW. There were relatively low levels of regenerating pure balsam fir stands (Fig. 1.4), as a consequence of the abundant conversion to mixedwood composition following harvesting. Nevertheless, with the low spruce stands abundance and age and the low softwood productivity of mixedwood stands, balsam fir stands remained the main source of softwood volume in 2004 (50% of total softwood volume; see Results). A combination of these factors explains why we did not find large differences in overall volume reduction levels between the 1985 and 2004 simulations.

This limited impact of forest management on forest vulnerability to the SBW over the medium term contrasts with correlative studies relating high SBW outbreak severities during the 20^{th} century to large-scale increases in the abundance of balsam fir following forest management (Blais 1983, Jardon et al. 2003, but see Boulanger et al. 2012). However, our results may not entirely address this question, as host connectivity or forest contiguity, which were not accounted for in our model, could play a role in determining the damage generated by SBW at the landscape scale (Robert et al. 2012). Nevertheless, our results suggest that variability in host resource abundance and age might not be as high as expected immediately following a severe SBW outbreak and that such high variability, if ever present, may be more visible over a multiple outbreak time frame.

In this study, we applied three SBW outbreak scenarios of varying severity on the forest resource in a top-down manner as input to SBWDSS projections, but host resource abundance and susceptibility at the landscape scale (as defined by host species and age) also determine regional SBW outbreak patterns (Cooke et al. 2007). Future studies could thus make use of bottom-up approaches, like regeneration/succession studies and process-based modeling, to explore the role of feedbacks between forest resource and SBW outbreak patterns in determining forest vulnerability to the SBW.

1.6.2 Role of hardwoods and intensive management in preventive strategies against SBW

Needham et al. (1999) found that optimum hardwood levels depend on the severity of SBW attack: below 45% defoliation (5 yr average), the amount of balsam fir volume lost to increased hardwood growing space exceeded the amount of volume protected, but as defoliation severity increased above 45%, the optimal hardwood levels increased. At severe levels of defoliation (>75%) optimal hardwood content was approximately 50% of initial standing volume (Needham et al. 1999). The mortality levels simulated by Needham et al. (up to 94% mortality), are most likely rare at the landscape level (but see MacLean and Ostaff (1989): average of 87% fir mortality in Cape Breton) as they are higher than the most affected stands in our study area (average of 52% volume reduction in the most vulnerable, balsam fir stands in the severe outbreak, no hardwood content effect). While our results also suggest a positive correlation between outbreak severity and hardwood content effect and despite mixedwoods being substantially less vulnerable when considering the protective effect of hardwoods (Fig. 1.7), we found that softwood stands still produced more softwood timber than mixedwood stands. Thus, increased hardwood content resulted in fewer softwood trees in the landscape, a loss of softwood timber that was never compensated for by the protective effect of hardwoods.

In unmanaged, SBW-prone forests, increases in hardwood content are temporary, as shade-tolerant balsam fir eventually takes over as the hardwood cohort gradually disappears (Holling 1973; Marchand 1991). However, the use of clearcut harvesting, which tends to promote shade-intolerant species (Harvey and Bergeron 1989), without plantation or competing vegetation control over successive forest rotations could maintain forest composition in an early successional stage. Our results suggest that intensive management with cleaning or vegetation management is necessary to limit hardwood encroachment and that the current rate of use of extensive management will eventually affect the sustainability of softwood timber production in the study area.

Most forest composition changes (mixedwood stand abundance increase and balsam fir stand abundance decrease) that occurred in the study area were unplanned, i.e. they resulted from earlier spruce budworm outbreaks or from natural regeneration following harvesting. The relatively limited extent of "planned" forest composition changes resulting from intensive management did not increase softwood volume in managed stands relative to unmanaged stands, but it contributed to limiting hardwood encroachment and softwood decline following harvesting (Fig. 1.8). This effect was particularly true for PCT, which maintained a balanced composition between the three stand types. In that sense, these results are in agreement with Belle-Isle and Kneeshaw (2007), who suggested that PCT in boreal mixedwoods can limit hardwood encroachment and emulate natural forest dynamics in terms of forest composition. This is especially the case for jurisdictions such as Quebec where herbicides (frequent alternatives to PCT) have been banned (Gouvernement du Québec 1998; Harvey and Brais 2002; Belle-Isle and Kneeshaw 2007). Nevertheless, the failure of intensive management in increasing spruce-fir stand abundance in the study area was clear and largely attributable to the low use vegetation management treatments in plantations (combined plantation and PCT treatments), which is a main factor determining intensive management effectiveness (Thompson and Pitt 2003). This raises questions about how preventive management against SBW and intensification of forest productivity are currently implemented in boreal mixedwoods of Quebec. Plantations must be successfully established and PCT must shift species composition from balsam fir toward spruce to be effective landscape-scale factors.

White spruce and especially black spruce plantations increased the post-outbreak softwood yield, with respectively 33% and 45% increases in post-outbreak yields relative to PCT (during a severe outbreak scenario with hardwood content effect; Fig. 1.9), but were often invaded by balsam fir and intolerant hardwoods, stressing the need for effective vegetation management or cleaning (Thompson and Pitt 2003; Wagner et al. 2006). Considering that economic constraints might limit the use of cleaning treatments on all plantations, it becomes necessary to evaluate the risk of hardwoods or balsam fir taking over the plantation. For instance, site quality or the pre-harvest hardwood content could serve as indicators of high competition risks (Harvey et al. 1995; Laflèche et al. 2000) and combined with cost/benefit analyses (Thompson and Pitt 2003), managers could thus make use of our softwood yield projections to select the best cost effective intensive management treatment in the context of SBW-prone forests.

White spruce is often preferred to black spruce for its higher wood value and productivity, but since we did not look at wood value and because of the identical black and white spruce undefoliated yield in our model, it is difficult to reliably recommend the best choice between black or white spruce because it depends upon the given situation. Nevertheless, the high post-outbreak softwood yields of cleaned and uncleaned black spruce plantations we found here and their lower vulnerability suggest that a balanced mix of plantations of black and white spruce, as well as minor or non-hosts conifer species, like in the study area (i.e. 32% black spruce, 41% white spruce, 12% Norway spruce, and 15% other species), represent a conservative and reasonable approach.

We did not observe significant effects of the 1985-2004 forest management activities on overall forest vulnerability to the SBW, due to factors including: the ineffectiveness of PCT and plantations in increasing spruce-fir content, the effective but limited use of cleaned plantation treatments, and the considerable softwood yield reduction that followed the large hardwood content increase. We rather observed a large decrease in softwood timber supply from 1985 to 2004, which was attributable to both the SBW and hardwood encroachment. Although the hardwood content effect was the highest in severe outbreaks, the protective effect never compensated for the loss of softwood growing space to hardwoods. We therefore question the strategy of increasing hardwood content in forests to reduce SBW damage and also question the widespread use of extensive management which generates a strong hardwood encroachment in boreal mixedwoods. Although we cannot recommend the most profitable option between black and white spruce plantation in revenue terms, our results suggest that the combination of black and white spruce plantation and cleaning treatments currently is the most effective solution to increase softwood yield and reduce forest vulnerability to the SBW. Thus, we stress the need for a more effective competing vegetation control and an increased abundance of spruce species and non-host softwoods in SBW prevention strategies.

1.7 ACKNOWLEDGEMENTS

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CHAPITRE II

FOREST HARVESTING AND SPRUCE BUDWORM OUTBREAKS CAUSE SIMILAR SHIFTS IN SPECIES DOMINANCE

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2.1. ABSTRACT

Forest management, natural disturbances such as insect outbreaks and their combined interaction affect recruitment and subsequent forest composition. A widespread increase in the proportion of hardwoods was observed following the last spruce budworm (SBW: *Choristoneura fumiferana* Clemens) outbreak in eastern Canada (1967-1992), but forest management can also increase hardwood abundance and its large-scale impact remains uncertain. To assess the relative large-scale effects of severe SBW damage and forest harvesting on forest composition, we evaluated changes in observed forest cover and projected volume yield at maturity in 1972-74 and 2004-2006 using three study areas in Quebec with varying softwood–hardwood content. Severe spruce budworm disturbance and harvesting had similar effects during the study period across study regions and increased overall hardwood content on 32% and 31% of the area, respectively. Surprisingly, hardwood content increase was further enhanced by harvesting in the landscape with the lowest initial hardwood content, with a net 48% area with increased hardwood content, relative to 21% of the area for the landscape with the highest initial hardwood content. Our results suggest that increased hardwood content occurred after both severe SBW damage and harvesting and suggest the overall presence of alternate softwood-mixedwood dominance dynamics within SBW-susceptible forests.

2.2. RÉSUMÉ

L'aménagement forestier, les perturbations naturelles telles que les épidémies d'insectes ainsi que leurs interactions affectent le recrutement d'arbres et, conséquemment aussi la composition forestière. Un accroissement accru dans la proportion de feuillus a été observé suivant la dernière épidémie de tordeuse des bourgeons de l'épinette (TBE: Choristoneura fumiferana Clemens) dans l'est du Canada (1967-1992), mais l'aménagement forestier est également tenu responsable de l'accroissement de la proportion de feuillus et son effet à grande échelle demeure méconnu. Afin d'évaluer l'effet relatif à grande échelle de la

mortalité sévère liée à la TBE et de la récolte forestière sur la composition forestière, nous avons évalué les changements observés du couvert forestier de 1972-74 et 2004-06 dans trois territoires du Québec suivant un gradient de composition conifère-feuillu. La TBE et la récolte forestière ont montré des effets similaires durant la période couverte et dans les trois régions étudiées en augmentant globalement la proportion feuillue de 32% et 31% de la superficie, respectivement. Étonnamment, l'accroissement en proportion feuillue a été accentué dans le paysage dominé par les résineux, avec un accroissement net de la proportion feuillue de 48% de la superficie par rapport à 21% dans le paysage dominé par les feuillus. Nos résultats suggèrent que tant l'épidémie sévère de TBE que la récolte forestière ont généré un accroissement significatif en proportion feuillue et suggèrent également la présence à grande échelle d'une dynamique alterne de dominance résineuse-feuillue dans les forêts susceptibles aux épidémies de TBE.

2.3. INTRODUCTION

Previous research has suggested that in balsam fir (Abies Balsamea (L.) Mill.)-dominated forests, spruce budworm (Choristoneura fumiferana Clemens (SBW)) outbreaks lead to cyclical succession with understory balsam fir abundant seedling bank replacing overstory balsam fir (Baskerville 1975, MacLean 1980). In maritime regions, balsam fir dominates natural stands as well as the forested landscape and thus recruitment is primarily of this species after spruce budworm outbreak, forest harvesting and even after fire (Kneeshaw et al. 2009). However, balsam fir decreases regionally from dominating the forest matrix in maritime forests to a being a companion species in forests in the Great Lakes region of central North America. Regional differences in canopy composition influence propagule availability and thus stand-level successional patterns (Taylor and Chen 2011). Cyclical succession of balsam fir to balsam fir would thus be expected to prevail in maritime regions where fir dominates, whereas greater compositional diversity in forests further to the west would lead to greater diversity in successional patterns.

Many authors have observed that SBW outbreaks provide recruitment opportunities for a large number of species in forests of Minnesota, Ontario and western Québec (Batzer and Popp 1985; Kneeshaw and Bergeron 1998; Bouchard et al. 2006; Taylor and Chen 2011). In a mixedwood forest in western Québec, temporal peaks in the regeneration of many co-occurring host and non-host species of varying shade tolerance were associated with previous outbreak periods (Bouchard et al. 2006). For example, Bouchard et al. (2006) found three temporal peaks in recruitment of shade intolerant or mid-tolerant species such as white birch (Betula papyrifera Marshall) and yellow birch (Betula alleghaniensis Britton) as well as shade tolerant fir and white spruce (Picea glauca (Moench) Voss) that coincided with three SBW outbreak periods over the 19th and 20th centuries.

Other work has, however, suggested that regional composition is not the driving factor in succession and that local stand level factors may have the largest impact on post-outbreak successional dynamics (Reyes et al. 2013). Specific events like SBW outbreaks in immature stands have been observed to promote recruitment of intolerant hardwoods (Spence and MacLean 2012). Baskerville (1975) also proposed that variation in successional patterns could depend on initial stand type. Local stand-level composition may be the primary driver of stand-level successional processes, but patterns may be tempered by regional species dominance. In other words, there may be a greater tendency for retrogressive succession (i.e. an increase in intolerant species in stands dominated by shade tolerant species before disturbance (Taylor and Chen 2011)) in fir stands embedded in a hardwood matrix and for progressive succession (i.e. an increase in tolerant species in stands dominated by shade intolerant species (Taylor and Chen 2011)) in hardwood stands located in a forest matrix dominated by balsam fir.

As well as regional and local influences, disturbance type affects forest succession (Reyes and Kneeshaw 2008). Stands naturally regenerated following forest harvesting can promote intolerant hardwood regeneration through increased vegetative reproduction (Safford et al. 1990) and increased light availability in harvest blocks (Harvey and Bergeron 1989). Carleton and MacLellan (1994) observed a conversion from conifer- to hardwood-dominated stands following harvesting. Alternatively, on sites with a well-established seedling bank, harvesting techniques promoting the maintenance of advance regeneration may lead to an increasing proportion of fir following harvesting (Blais 1983; James et al. 2010).

Forest management planning requires a strong understanding of future stand composition and thus our objectives are to compare successional change following two types of disturbance, forest harvesting and SBW outbreaks. Specifically, our goal was to evaluate the effects of the 1967-1992 SBW outbreak and forest harvesting on forest composition and volume at maturity (30 years after the outbreak started) in three study areas along a hardwood vs. fir content gradient from western (continental) to eastern (maritime) Quebec in the SBW-susceptible forest zone. We expect 1) fir content will increase in naturally (SBW) disturbed stands following Baskerville (1975) cyclical succession hypothesis, 2) hardwood content will increase in all stand types following harvesting, and 3) fir increases will be greatest for all stand types after SBW in the fir-dominated eastern study area and smallest in the western study area where the forest matrix is dominated by companion species, and the opposite (i.e. greater hardwood increase in the continental study area than the maritime study area) will occur following harvesting.

2.4. METHODS

2.4.1. Study area

We studied stand types in three study areas, all part of the balsam fir-dominated forest of Quebec and susceptible to SBW outbreaks, but with different species dominating the regional forest matrix: (1) the Abitibi (western, continental climate) hardwood-dominated study area of 112 000 ha, (2) the Mauricie (central) black spruce-dominated (Picea mariana (Mill.) B.S.P.) study area of 304 000 ha, and (3) the Gaspésie (eastern, maritime climate) balsam fir-dominated study area of 103 000 ha. They are located along several environmental gradients from west to east: an increasing precipitation gradient, a decreasing hardwood content gradient, an increasing balsam fir content gradient, and an increasing SBW outbreak severity gradient. Gray et al. (2000) determined the SBW outbreak impact class for the three study areas as negligible to severe (1-2 years to >10 years of high defoliation), low to severe (3-5 years to >10 years of high defoliation), and moderate to severe (6-10 years to >10 years of high defoliation) for the hardwood-, spruce-, and fir-dominated study areas, respectively. Areas are located along a 1 000 km-long axis, between 79° 31' – 65° 51' west and 47° 38' – 48° 42' north. Precipitation increases from a mean of 850 mm in the continental study area to 900-1200 mm in the maritime study area (Environment Canada 2008). All study areas were substantially affected by forest management, with 35%–51% of stands harvested from 1972-1974 to 2004-2006, 25%–26% of stands naturally regenerated, and 10%–14% of stands with plantation, tending, or both treatments. In all three study areas, the most common species are balsam fir, black spruce, and intolerant hardwoods (mainly paper birch (Betula papyrifera Marshall) and trembling aspen (Populus tremuloides Michx.)) although their proportions vary. Other softwood species, including mainly jack pine (Pinus banksiana Lamb.), tamarack (Larix laricina (Du Roi) K. Koch), and eastern white cedar (Thuja occidentalis L.), together compose 13%, 19%, and 2% of total stems found in local permanent and temporary sample plots (within 50 km of study area; n=94, 330, and 183 plots for the hardwood-, black spruce-, and balsam fir-dominated study areas, respectively).

2.4.2. Data source of stand characteristics

Data were collected on forest cover composition, stand age, stand volume, and disturbance (harvesting, insect outbreak, fire, and windthrow). Forest composition for each of the study areas was determined from the SIFORT database (Pelletier et al. 2007) at two points in time: 1972-1974 and 2004-2006. The SIFORT database records, in a 14 ha-resolution grid, forest composition as the leading species, stand density, average height, and disturbance type and year. The first SIFORT inventory, hereon referred to as the pre-outbreak inventory, coincided approximately with the beginning of the last SBW outbreak in the three study areas (1971-1973) and the second inventory, hereon referred to as the post-outbreak inventory, was conducted 12-21 years after the outbreak ended. Specifically, as reported by aerial defoliation surveys, the SBW outbreak lasted from 1971-1985, 1971-1986, and 1973-1992 in the hardwood-dominated, spruce-dominated, and fir-dominated study areas, respectively. As SBW-caused mortality begins 4 to 5 years after the beginning of the outbreak (MacLean 1980), the first SIFORT inventory represents pre-outbreak stand conditions.

To characterize forest composition changes in each study area, we divided areas into five stand types based on species dominance: balsam fir stands (≥75% in forest cover), spruce–fir stands (spruce ≥50% and balsam fir ≥25%), softwood-hardwood stands (softwoods ≥50% and hardwoods ≥25%), hardwood-softwood stands (hardwoods ≥50% and softwoods ≥25%), and hardwood stands (≥75% hardwoods). 30%–44% of the total sampled points in the three study areas had unknown composition either in the pre- or post-outbreak inventory and were not considered in the analyses; we thus had 66,164 ha, 170,176 ha, and 68,222 ha with known composition for the hardwood-, spruce-, and fir-dominated areas, respectively. Distinction was not always made between dominant softwood species in the SIFORT database and consequently, we decided to group all softwood species together and analyze the softwood component as a whole.

Aerial stand inventory such as SIFORT provide coarse, large-scale trends in composition changes often reported from remote sensed data (D'Aoust et al. 2004; Vepakomma et al. 2011). However, because of the categorical nature of stand data in terms of dominant composition (four classes: 0%–24%, 25%–49%, 50%–74%, 75%–100%), we determined whether the softwood content class of stands either decreased, increased, or stayed the same from the pre-outbreak to post-outbreak inventories. We thus assessed composition change using absolute and relative proportions of area with softwood increase or decrease.

2.4.3. Identification of harvested and SBW-attacked stands

The SIFORT data base was used to identify stands that were harvested and stands that had severe mortality following the SBW outbreak. Forest management activities occurred throughout and after the SBW outbreak, but for purposes of comparison with forest composition change in SBW-affected stands, we only used stands harvested during the outbreak (up to the last year of reported aerial defoliation). A vast majority (mean 94%) of harvested area was also affected by SBW disturbance to some degree. The combination of SBW and harvesting likely represents salvage logging treatments (SBW followed by harvesting) and/or pre-salvage logging treatments and/or SBW-caused damage to immature stands (harvesting followed by SBW damage; Ruel and Huot 1993). Many distinctions have been observed in the literature between the impact of harvesting and SBW disturbance on stand composition, therefore we grouped all harvested stands together and considered two disturbance types: harvesting (all cases where harvesting took place) and severe SBW-only affected stands.

In addition to SIFORT data, we used aerial defoliation estimates (nil (0%), light (1%–34%), moderate (35%–69%), and severe (70%–100%)) conducted annually in Quebec (Ministère des forêts de la faune et des parcs 2015) to describe SBW outbreak severity by study area and by stand type. To assess potential SBW-related mortality, we determined cumulative defoliation based on annual defoliation class midpoints (0%, 18%, 52%, and 85%), which were summed for each defoliation year at each sample point in the forest database. As Blais (1958) found that 75% mortality was associated with a range or 550 to 800% cumulative defoliation, we used the midpoint (675%) cumulative defoliation to validate the identification by the SIFORT database of stands with >75% SBW-caused mortality (severe mortality).

2.5. RESULTS

Cumulative defoliation across study areas reflected an increasing gradient in outbreak severity from west to east (host and non-host stands combined), ranging from 0% to 855% (mean 323% ± 266% standard deviation) in the hardwood-dominated western area, to 0% to 1093% (mean 582% ± 232%) in the black spruce-dominated central area, and to 364% to 1110% (mean 717% ± 143%) in the balsam fir-dominated eastern area, in congruence with the regional shift in dominance of hardwoods to fir along the west-east forest range in Québec. Mean cumulative defoliation was the highest in balsam fir stands for the hardwood- and spruce-dominated study areas, and in spruce-fir stands for the fir-dominated study area (which only represented 1% of total area) with 540%, 768%, and 725% for the hardwood-, spruce-, and fir-dominated study areas, respectively (Fig. 2.1). Nevertheless, balsam fir stands in the fir-dominated study area were among the most affected stand types with 703% cumulative defoliation. The lowest cumulative defoliation values were found in hardwood (hardwood-dominated and fir-dominated study areas) and spruce-fir stand types (spruce-dominated study area) with 191%, 492%, and 517% for the hardwood-dominated, spruce-dominated, and fir-dominated study areas, respectively.

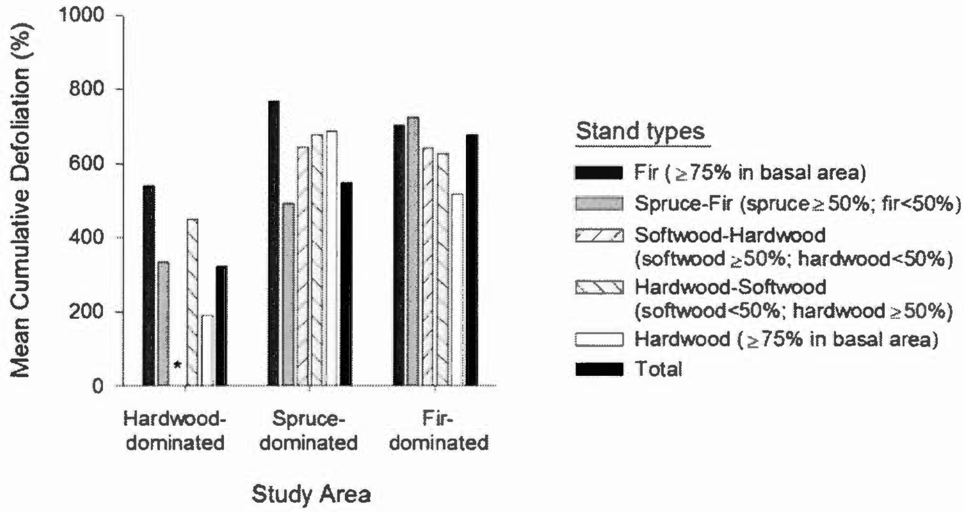

Figure 2.1. Mean percentage cumulative defoliation from 1971 to 1992 per stand type (fir, spruce-fir, softwood-hardwood, hardwood-softwood, hardwood, and total) and study area (Hardwood-dominated, Spruce-dominated, and Fir-dominated). Hardwood stands shown here include up to 24% of SBW host species (fir or spruce). Asterisks show nonexistent stand types for which information was not available.

Together or separately, severe SBW mortality and harvesting occurred on 28%–38% of each study area during the study period (Table 2.1; only applies to the area with known species composition). The remaining area consisted of other disturbances: light/moderate spruce budworm-caused mortality only (<75% mortality; 37%–51% of each study area), no disturbance (0%–18%), intensive management (10%–14%), and wildfires and other infrequent natural disturbance (1%–11%).

Tableau 2.1. Distribution of area by stand types at the time of the pre-outbreak inventory (1972-1974) for the three study areas as a function of disturbance that occurred between the pre- and post-outbreak (2004-2006) inventories: severe spruce budworm-caused mortality and harvesting.

Pre-outbreak stand type	Study areas, ha (% of study area in italic)		
	Hardwood-dominated	**Black spruce-dominated**	**Balsam fir-dominated**
Balsam fir	**12 404** *(19%)*	**2 604** *(2%)*	**43 904** *(64%)*
Severe SBW mortality	*372*	*286*	*5 268*
Harvesting	*4 341*	*677*	*10 098*
Spruce-fir	**11 382** *(17%)*	**96 166** *(56%)*	**910** *(1%)*
Severe SBW mortality	*228*	*9 617*	*164*
Harvesting	*2 504*	*25 965*	*100*
Softwood-hardwood	-	**19 726** *(11%)*	**11 256** *(17%)*
Severe SBW mortality	-	*2 959*	*563*
Harvesting	-	*4 340*	*2 701*
Hardwood-softwood	**24 864** *(38%)*	**40 460** *(24%)*	**9 730** *(14%)*
Severe SBW mortality	*995*	*5 664*	*487*
Harvesting	*8 702*	*8 497*	*2 724*
Hardwood	**17 514** *(26%)*	**11 760** *(7%)*	**2 422** *(4%)*
Severe SBW mortality	*175*	*1 176*	-
Harvesting	*3 853*	*3 528*	*775*
Total	**66 164**	**170 716**	**68 222**

Notes: stand types were grouped and initially defined based on forest cover proportion: balsam fir (≥75% balsam fir), spruce-fir (≥50% black spruce, ≥25% balsam fir), softwood-hardwood (≥50% softwood, ≥25% hardwood), hardwood-softwood (≥50% hardwood, ≥25% softwood), and hardwood stands (≥75% hardwood). Severe SBW mortality was defined as stands with ≥ 75% basal area in mortality.

2.5.1. Softwood cover change between the pre- and post-outbreak inventories

The vast majority of the disturbed area had a net decline in softwood content between 1972-74 and 2004-06, across all disturbance types and study areas, ranging from a net softwood reduction on 60% of the area for SBW-affected stands in the fir-dominated study area to a net softwood increase on 33% of the area for harvested stands in the hardwood-dominated study area (Fig. 2.2). The effect of harvesting on softwood cover change was generally similar to that of severe SBW mortality across stand types and study regions, with overall decreased softwood cover in softwood stands ranging 18%-96% and 42%-96% of the area for SBW-affected and harvested stands, respectively, and overall increased softwood cover in hardwood and hardwood-dominated stands ranging 26%-64% and 20%-62% of the area for SBW-affected and harvested stands, respectively.

For both SBW disturbance and harvesting, post-disturbance stand softwood content gradually decreased as hardwood content in the landscape decreased, with net softwood increase on 10% of the area, and net softwood decrease on 25% and 60% of the area for SBW-affected stands and softwood decreases on 27%, 29%, and 44% of the area for harvested stands within hardwood-dominated, spruce-dominated, and fir-dominated study areas, respectively (Fig. 2.2). This inverse relationship between landscape hardwood content and post-disturbance stand softwood content is also enhanced by the fact that the only two cases of net softwood content increase were found in the hardwood-dominated study area, with net softwood increases on 10% and 33% of the area following SBW disturbance and harvesting disturbances, respectively.

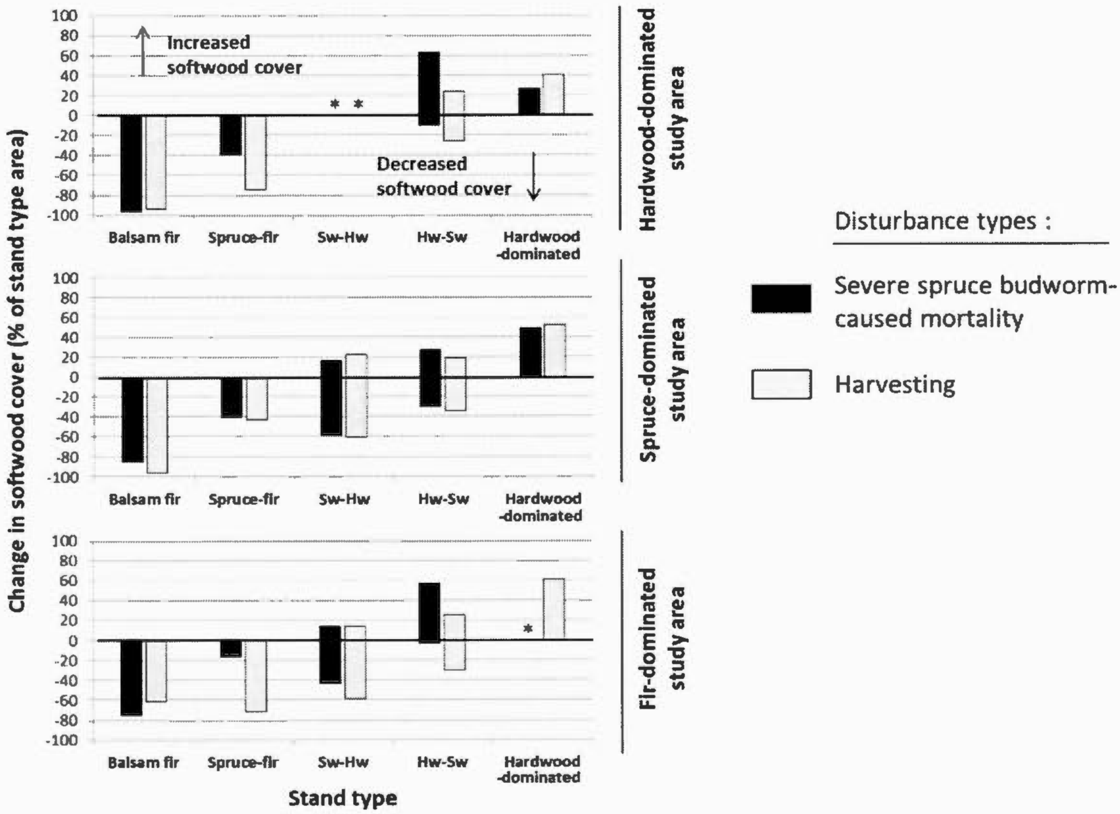

Figure 2.2. Percentage of the three study areas with softwood cover increase or decrease between the pre- and post-outbreak inventories by stand type (balsam fir, spruce-fir, softwood-hardwood (Sw-Hw), hardwood-softwood (Hw-Sw), and hardwood-dominated) and disturbance type (severe spruce budworm-caused mortality and harvesting). Asterisks show nonexistent stand types for which information was not available.

2.6. DISCUSSION

2.6.1. Softwood content change after spruce budworm or harvesting

Consistent with expectations, softwood cover decreased in softwood-dominated stands following harvesting and SBW. The fact that changes were strongest in fir-dominated stands and that spruce-dominated stands underwent much less change (the majority remained the same) is consistent with balsam fir being the primary host of the spruce budworm and black spruce a secondary host (Hennigar et al. 2008). However, it also shows that these stands are the most vulnerable to hardwood encroachment and thus may not directly follow cyclical dynamics of fir replacing fir (Baskerville 1975a; MacLean 1980).

The effect of hardwood encroachment is strongest in the hardwood-dominated area, but is present across all study areas. This phenomenon has been described after harvesting (Harvey and Bergeron 1989; Carleton and MacLellan 1994), but more rarely after SBW. Earlier research has suggested that SBW outbreaks may be important mechanisms to maintain early successional species in older stands (Kneeshaw and Bergeron 1998; Bouchard et al. 2006), but none of these authors noted such a large response (but see Bergeron (2000)).

We expected softwood cover to increase over the study period following SBW in hardwood-dominated stands, since advanced shade-tolerant regeneration should take advantage of openings caused by either mortality of fir and spruce trees or by senescence of hardwoods over the study period (Senecal et al. 2004). However, unexpectedly, harvesting did not systematically lead to hardwood encroachment and SBW outbreaks did not systematically lead to conifer recruitment in pre-disturbance conifer-dominated stands. Although many stands maintained the same composition, retrogressive successsion was often observed after severe SBW-caused mortality in conifer stands.

2.6.2. Sustainability of softwood production within SBW-affected forests

The concern that forest harvesting modifies forest composition and eventually softwood yield has been a driver for proponents of forest management strategies to emulate natural disturbances (Gauthier et al. 2009). However, our observations suggest that concerns about different composition cover changes between SBW outbreaks and harvesting may not always be founded. We generally observed a similiar impact of forest harvesting relative to SBW on forest composition.

Our observations are based on a 30-year period and impacts may evolve differently over a longer term or given lighter SBW outbreaks. The change analysis that we used suggests that these forests are dynamic, but despite softwood cover reductions in softwood stands and hardwood cover reductions in hardwood stands, these two stand types generally maintained their respective dominances (Holling 1973). Further research will be needed to assess the relative probabilities of hardwood encroachment and cyclic fir-fir succession at an operational, stand level and to eventually guide sustainable forest management in SBW-susceptible forests.

2.7. ACKNOWLEDGEMENTS

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CHAPITRE III

EFFECTIVENESS OF PREVENTIVE FOREST MANAGEMENT STRATEGIES IN REDUCING THE SEVERITY OF SIMULATED SUCCESSIVE SPRUCE BUDWORM OUTBREAKS

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3.1. ABSTRACT:

It has been suggested that the severity of spruce budworm (SBW) outbreaks can be influenced by composition manipulations to non-host or secondary host species at the stand level or by host configuration at the landscape-scale. To evaluate the potential impacts of forest composition manipulation at the landscape scale on SBW disturbance, a stochastic landscape simulation model (LANDIS-II) was used on a 3 600 km^2 boreal forest landbase in central Quebec, Canada. Three management strategies were simulated (unmanaged, increased hardwood (non-host) and increased black spruce (*Picea mariana* Mill.; secondary host) abundance) and their impact on biomass reduction due to SBW-caused mortality in three successive outbreaks were simulated. Management strategies were evaluated in terms of mean and cumulative damage due to mortality, and in the likelihood of moderate/severe mortality. Although mortality levels were low, the increased spruce scenario was the most effective in decreasing overall damage in the three outbreaks; only 3% mean biomass reduction occurred in the spruce scenario relative to 5% and 9% for the increased hardwood and unmanaged scenarios, respectively. Despite an overall reduction in mortality across the entire landscape after management, the opposite was found in balsam fir (*Abies balsamea* (L.) Mill.; preferred host) stands. Biomass reductions (1.4-fold increase) and likelihood of moderate/severe mortality (1.5-fold increase) were higher in the managed scenarios relative to the unmanaged scenario after successive outbreaks but fewer balsam fir stands occurred on the landscape. Our study landscape was initially a mixed-forest and this may have contributed to the effectiveness of management; analysis with longer outbreak series and on areas with higher fir content will be required to evaluate if these treatments should be of concern.

3.2. RÉSUMÉ:

Il est suggéré que la sévérité des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) peut être influencée par des manipulations de composition visant à augmenter l'abondance d'espèces non-hôtes ou hôtes secondaires ou par la configuration des hôtes à l'échelle du paysage. Afin d'évaluer l'impact potentiel des manipulations de composition sur la perturbation par la tordeuse à l'échelle du paysage, un modèle de simulation stochastique (LANDIS-II) a été utilisé sur un territoire de 3 600 km^2 situé en forêt boréale, au centre du Québec, Canada. Trois stratégies d'aménagement ont été simulées (aucun aménagement, feuillus accrus (non-hôtes) et épinette noire accrue (*Picea mariana* Mill.; hôte secondaire)) et leurs impacts sur les réductions de biomasse causées par la mortalité liée à la tordeuse lors de trois épidémies successives ont été simulés. Les stratégies d'aménagement ont été évaluées en termes de dommages moyens et cumulatifs liés à la mortalité par la tordeuse et en termes de vraisemblance de mortalité modérée/sévère. Malgré que les niveaux de mortalité sont demeurés bas, le scénario d'épinette accrue s'est révélé être le plus efficace à réduire les dommages totaux suite aux trois épidémies successives; il y eut seulement 3% de réduction en biomasse moyenne dans le scénario d'épinette accrue comparativement à 5% et 9% pour le scénario de feuillus accrus et celui sans aménagement, respectivement. Malgré une réduction de mortalité totale à travers le paysage après aménagement, le contraire a été obtenu dans les peuplements de sapin baumier (*Abies balsamea* (L.) Mill.; hôte préféré). Les réductions de biomasse (1.4 fois plus élévées) et la vraisemblance de mortalité modérée/sévère (1.5 fois plus élevée) se sont accrues pour les scénarios incluant de l'aménagement forestier après les trois épidémies successives, bien que l'abondance de peuplements de sapin baumier était fortement diminuée. Notre aire d'étude était initialement composée de forêt mixte, ce qui a pu contribuer à l'efficacité de l'aménagement; des analyses couvrant une période plus longue et sur des territoires où le sapin baumier est plus abondant seront requises pour évaluer s'il faut être prudent avec ces stratégies de modification de composition.

3.3. INTRODUCTION

The spruce budworm (*Choristoneura fumiferana* [Clem.]) disturbance regime is one of the most studied systems and despite strong stand-level responses to composition manipulations, there is debate about the effect of large-scale composition manipulation by forest management on SBW outbreaks (Miller and Rusnock 1993; Koricheva et al. 2006). A debate that obviously extends beyond the simple rule that a reduction in hosts will reduce food and thus outbreak severity (Kneeshaw et al. 2015). Blais (1983) and Anderson et al. (1987) suggest that forest management has increased host content and led to more severe and frequent outbreaks than in the past. Boulanger and Arsenault (2004) suggest that outbreak patterns are regular over four centuries, while James et al. (2010) suggest that forest management tends to reduce vulnerability to the SBW when compiled across a landscape and over time. It has also been suggested that where a previous SBW outbreak was severe, the next SBW outbreak could be less severe due to increased hardwood content and reduced balsam fir stand age (Bouchard et al. 2006).

The main focus of forest pest management strategies reducing stand vulnerability is to reduce host species abundance. Feedbacks between insect populations and stand composition may also scale up to influence regional differences in outbreak characteristics (Sturtevant et al. 2015). In the spruce budworm system, two alternative strategies have been proposed: (1) replace the primary host species (balsam fir (*Abies balsamea* (L.) Mill.) with a less vulnerable, secondary host species (black spruce) and (2) increase the proportion of hardwoods in the forest. Hardwoods have been shown to offer a protective effect to nearby hosts (Su et al. 1996) through natural enemy and dispersal loss effects (Sturtevant et al. 2015). It is questionable, however, whether the reduction of defoliation caused by increased hardwood content will result in a higher softwood timber supply than without hardwoods (Sainte-Marie et al. 2015). Mixtures of fir and black spruce (*Picea mariana* Mill.) may also lead to longer outbreaks as the insect switches or spills over from the primary host to a secondary host as the primary food resource is depleted (White and Whitham 2000;

Bognounou et al. In review). However, short-term and stand-level effects may not directly scale-up to landscape-level effects over multiple forest rotations.

The objective of this study is to compare at the landscape scale the effectiveness of forest composition manipulation scenarios to unmanaged forests in reducing damage related to the SBW over successive outbreaks. Through a prolonged and constant impact on forest composition, it is expected that forest management will stabilize outbreak severity and reduce the abundance of balsam fir, but in the presence of repeated SBW outbreaks, these expectations may not hold. If this is the case, efforts to reduce the influence of SBW outbreaks through composition manipulation may be a cost-inefficient strategy that requires much effort to reap small or negligible benefits over multiple outbreaks. Using forest dynamics modeling, we quantify the potential effects of increasing hardwoods or black spruce vs. doing nothing on host species mortality after three consecutive outbreaks across a forested landscape. In other words, if we had the capacity to radically change forest composition at the landscape scale, what would be the consequences on host mortality under a stationary outbreak regime?

3.4. METHODS

3.4.1. Study area

We used a 262,000 ha mixedwood forest management unit located in central Quebec, Canada, mostly composed of balsam fir, black spruce, and white birch (*Betula papyrifera* Marshall) (Fig. 3.1). Other SBW hosts like white (*Picea glauca* (Moench) Voss) and red spruce (*Picea rubens* Sarg.) are infrequent, accounting for <6% of total merchantable stems (DBH > 9 cm; 1478 stems) in QMFFP (Quebec Ministry of Forest, Wildlife, and Parks) permanent sample plots (86 plots measured either in 2007 or 2010) and temporary sample plots (265 plots measured in 1999) found within 50 km of the study area. Non-host conifers are also infrequent, with <6% of total reported individuals in the selected plots.

The area is subject to recurrent SBW outbreaks with three outbreaks being recorded in the 20th century (around 1910, 1950 and 1980), with the 1950 outbreak being the most severe in the region (Bouchard et al. 2007). Although the fire regime has not been locally studied, the current (> 1920) and historical (< 1850) fire return interval just west of the St-Maurice River (Fig. 3.1) was estimated at 273 and 69 years, respectively (Bergeron et al. 2001). Since other fire-dependent species are rare (jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.)), Bouchard et al. (2007) approximated the fire return interval east of the St-Maurice River to be higher than 200 years, similar to the lower St-Maurice Valley (Barrette 2004). Other natural disturbances (windthrow and hardwood dieback) had little influence, covering < 3% of the study area from 1972 to 2006, according to the SIFORT database, a 14 ha-resolution systematic sampling grid based on stand information (Pelletier et al. 2007).

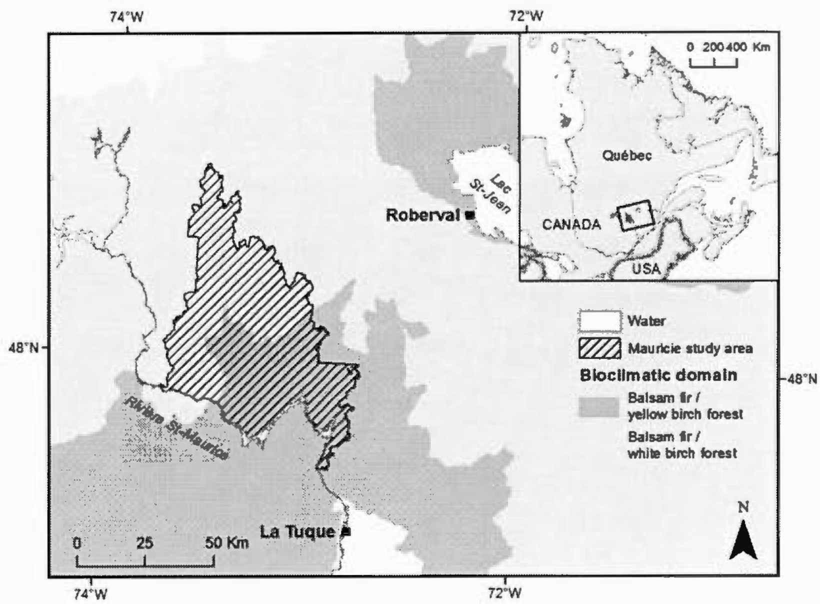

Figure 3.1. Map of the Haute-Mauricie region and study area, overlapping two balsam fir bioclimatic zones.

3.4.2. Simulation modeling

3.4.2.1. Model description

We used the LANDIS-II spatial landscape disturbance simulator (Scheller et al. 2007), an established model that can address the complex issue of forest management and spruce budworm interactions over successive outbreaks. Its spatial structure enables the simulation and interaction of forest processes and disturbance, i.e. forest succession, SBW outbreaks and forest management in the present study, and allows their interaction through forest composition and age (Fig. 3.2). Landscapes are represented as grids of cells (or sites; 10-ha resolution in this case), which have homogeneous light environments, and are aggregated into ecoregions with homogeneous climate and soils (8 ecoregions in this case). Forest composition at the cell-level is represented as age cohorts of individual tree species that interact via a suite of vital attributes (e.g. shade tolerance, seed dispersal, ability to sprout vegetatively, longevity, etc.) to produce nondeterministic successional pathways sensitive to disturbance type and severity. Extensions interact with each other through species composition and age, adding cohorts or removing cohorts or portions of cohort biomass (cohort- and biomass-based extensions; forest succession and harvesting extensions in this case) or in removing whole cohorts only (cohort-based extensions; SBW outbreaks extension in this case). The only model output we used is biomass (g/m^2) per species, per time step (year) and per site (Fig. 3.2d). An annual time step was used for all extensions.

Species are allowed to establish at any time step, if the site shade class permits it and if site biomass has not reached its maximum (equal to the biomass of the most productive species in the ecoregion), following the biomass succession extension assumptions (Scheller and Mladenoff 2004). Cohort reproduction rules give precedence to planting (if selected), then to resprouting (if vegetatively reproducing species were present before disturbance), and lastly to seeding if seed sources are found nearby (given effective and maximum seeding distance parameters; see He and Mladenoff (1999) and Scheller et al. (2007)).

Spruce budworm disturbance was simulated using the Biological Disturbance Agent (BDA) extension (v2.0.2; Sturtevant et al.(2004)). Insect outbreaks occur at intervals specified by a mean and standard deviation estimated from historic records. The BDA has to simplify several aspects of SBW dynamics in order to integrate both local and landscape-scale processes. Among them, SBW-caused cohort mortality is assumed to occur in a single simulation period (i.e. one year in this case).The BDA does not allow partial cohort mortality, but in order to reproduce the patchy mortality due to SBW at the landscape-scale (Kneeshaw and Bergeron 1998), the model uses probabilistic cohort mortality (cohort vulnerability). To determine whether a cohort is killed, the BDA first estimates the probability of disturbance for a given site, and if disturbed, cohort mortality probability defines the ability of the disturbance to kill host cohorts present on the site. The probability of disturbance (range 0–1) is calculated for all forested sites based on the regional defoliation level (range: 1 (light) to 3 (severe)) and on "site susceptibility value", i.e. the average value of the oldest cohort of each tree species per site as a food resource for the insect, based on empirical host susceptibility parameters (Hennigar et al. 2008). A species may be ignored (no effect on site vulnerability) or included in the estimation of site vulnerability value (range: 0 (non-host) to 1 (primary host)) (see Equation 1 in appendix). Vulnerability value for each site is ultimately averaged with nearby sites to include the vulnerability of surrounding sites (see *Model Parameterization*).

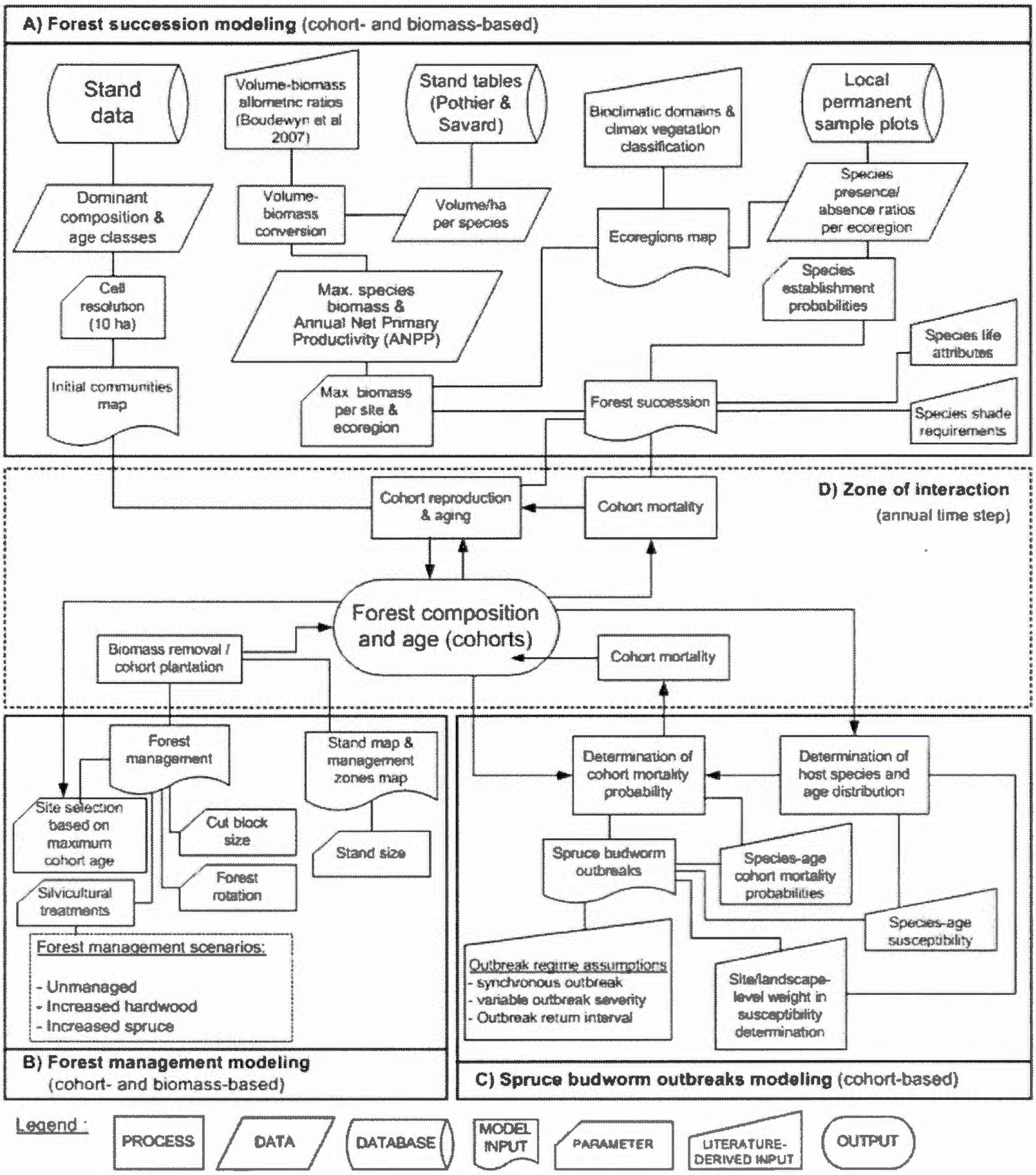

Figure 3.2. Data flow chart of the LANDIS simulations, based on tree species-age cohorts reproduction, aging, and mortality using three model extensions: (A) forest succession, (B) forest management, and (C) spruce budworm outbreaks. Extensions (D) interact with each other through species composition and age, in adding cohorts or removing cohorts or portions of cohort biomass (cohort- and biomass-based extensions) or in removing whole

cohorts only (cohort-based extensions). Spruce budworm outbreaks are assumed synchronous in the landscape, of stochastically varying severities, and occur at a 28 ± 13 years interval (Robert et al. 2012). Forest management scenarios represent large-scale composition changes strategies: unmanaged, increased hardwood (plantation of 25% white birch, 25% aspen, 25% fir, and 25% spruce over 80% of harvested area), and increased spruce (plantation of black spruce over 100% of harvested area). Cell resolution is 10 ha, i.e. stand-level resolution, and time step is annual.

3.4.2.2. Model Parameterization

3.4.2.2.1. Initial conditions, land types, and successional processes

We used the aerial photo-based inventory of forest characteristics of the QMFFP in order to obtain information on stand dominant species composition and age dating from 2006. The database records information on stands >4 ha and also contains stand-level information about initial and partial disturbance. Initial communities were obtained by converting stand-level data into 10-ha resolution sites and combining all the underlying species and age information from the stand database into each site (Fig. 3.2a). We divided the landbase into 8 ecoregions based on classification of potential site vegetation (sugar maple/yellow birch; yellow birch/balsam fir; balsam fir/white birch; balsam fir/black spruce; black spruce/lichen, and black spruce/moss) and regional bioclimatic zones (balsam fir-yellow birch forest and balsam fir-white birch forest domains) (Robitaille and Saucier 1998) (Fig. 3.3).

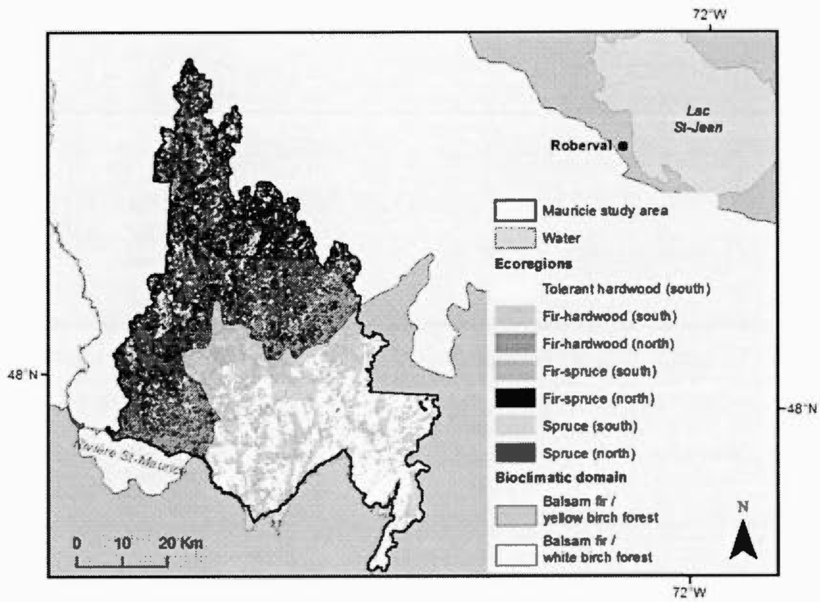

Figure 3.3. Ecoregions (8) map for the study area, divided in North and South regions: 1 & 2) tolerant hardwoods (sugar/maple yellow birch), 3 & 4) fir-hardwood (white birch), 5 & 6) fir-spruce, and 7 & 8) spruce (black spruce lichen/moss).

Estimates of species establishment probabilities were empirically-based and defined as species presence/absence ratio for seedlings (DBH < 2 cm), saplings (DBH: 2-9 cm), and trees (> 9 cm) sampled within surrounding QMFFP permanent sample plots (PSP) (n=84; found within 10 km of study area) and temporary sample plots (TSP) (n=606; found within 50 km of study area) inventoried between 1974 and 1999 (Fig. 3.2a). Data from the various life stages were pooled for each ecoregion to make sure we had realistic probabilities of both tolerant and intolerant species. The area being substantially managed (forest rotation: 60-90 years); PSPs are not spared from management), there should be adequate light for intolerant species to be represented in the pooled data set.

The biomass succession extension also requires parameters of maximum biomass and maximum above-ground net primary productivity (ANPP) per species. We derived estimates for each species for the North and South portions of the study area, following bioclimatic zones (see Fig. 3.1). Both maximum biomass and maximum ANPP parameters were estimated using region-specific stand growth tables from Pothier and Savard (1998), but in the absence of information on site quality, we used average site index but high stand density. Volumes were converted to biomass (for use in the biomass succession extension) based on allometric equations developed by Boudewyn et al. (2007) (Fig. 3.2a).

3.4.2.2.2. Disturbance regimes

Spruce budworm outbreaks were assumed to occur synchronously across the entire landscape (Royama 1984; Cooke et al. 2007) as large regional outbreaks have occurred in the past in the study area (Bouchard et al. 2007). Regional defoliation severity varied from light [1] to severe [3]), in conformity with the variability in past SBW outbreak severity in nearby areas (Bouchard et al. 2007; Morin et al. 2007). Intervals between outbreaks are probabilistic in the model and vary based on a mean and standard deviation estimated from Robert et al. (2012) in Ontario and Minnesota, i.e. a 28 ± 13 years (managed and unmanaged forests from 1910 to 2000), similar to the 25-40 years interval found in Eastern Canada (Royama 1984; Jardon 2001).

Species susceptibility values were estimated using percentage defoliation values relative to balsam fir, SBW preferred host (Hennigar et al. 2008) (Table 3.1). Probabilities of cohort mortality were based on percentages of tree mortality at the stand-level (MacLean 1980). Age-specific probabilities of mortality were based on a rule of thumb proposed by MacLean (2004), with balsam fir and spruce mortality in immature stands being reduced to a half relative to that in mature stands.

Tableau 3.1. Spruce budworm disturbance extension parameters.

Species	Species susceptibility value			Probability of cohort mortality					
				Light outbreak		Moderate outbreak		Severe outbreak	
Age classes:	0-19	20-39	40+	20-49	50+	20-49	50+	20-49	50+
Balsam fir	0.25	0.5	1.0	-	0.85	0.42	0.85	0.42	0.85
White spruce	0.18	0.36	0.72	-	0.42	0.15	0.42	0.15	0.42
Red spruce	0.1	0.20	0.41	-	-	-	0.36	0.13	0.36
Black spruce	0.07	0.14	0.28	-	-	-	0.36	0.13	0.36
Hardwoods	0	0	0	-	-	-	-	-	-
Non-host conifers	-	-	-	-	-	-	-	-	-

Notes: Species susceptibility value (range 0-1) is averaged among the oldest cohorts present on each site (see Methods). Hardwood species (value=0) decrease site average susceptibility value (Su et al. 1996) (i.e. protective effect), while non-host conifers are assumed neutral and do not influence site susceptibility value calculation. The model assuming that host cohorts either survive or die from an outbreak, patchy mortality observed at the landscape-scale is emulated by probabilities of cohort mortality (Sturtevant et al. 2004), based on stand-level % tree mortality values (MacLean 1980). Cohort mortality probabilities imply that only the most vulnerable hosts die during light outbreaks, while the least vulnerable hosts die only during severe outbreaks. Outbreaks are assumed to occur synchronously across the entire landscape (Royama 1984) and have a neighborhood radius of 1 km (this defines the number of adjacent cells used to estimate site susceptibility) (Campbell et al. 2008).

A hardwood content effect in reducing spruce-fir defoliation was implemented in the calculation of site susceptibility value, where hardwoods in a given site and in surrounding sites reduce the average site susceptibility value. Neighborhood influence on site susceptibility value was limited to a 1-km distance, as suggested by Campbell *et al.* (2008). The model allows users to specify the relative weight given to site and landscape-level composition on susceptibility to the SBW and as suggested by Campbell et al. (2008), we assigned a dominant weight (90%) to site susceptibility relative to landscape susceptibility (10%). Considering that dispersal of natural enemies of the SBW is still not well understood

(Cooke et al. 2007), a sensitivity analysis assigning a dominant landscape weight (90% landscape, 10% site) to the susceptibility value was also conducted, to assess the impact of higher natural enemy dispersal (Roland and Taylor 1997). However, the difference in mean prevented biomass reductions between the two scenarios remained within 10% for both the unmanaged and increased hardwood scenarios, i.e. scenarios with the highest hardwood content (see Appendix 1). Thus, the site-dominant (90% site, 10% landscape) settings were selected for the following analyses.

Forest management activities were simulated using the biomass harvest extension (v2.1; Gustafson et al. 2000). Clearcuts were implemented over a 70-year forest rotation period, similar to other managed areas in the balsam fir-dominated zone of Québec (60-80 years). Sites with the highest mean cohort age were selected for harvest each year, with a mean annual harvest rate of 1.4% of the study area (i.e. 4 330 ha/year). Yet, SBW-caused cohort mortality will inevitably reduce mean cohort age on affected sites, and potentially delay harvesting of these sites. Mean cut-block size was 74 ha ± 31ha standard deviation (minimum: 10ha, maximum: 160ha) similar to local regulations (30% of stands >50ha, Maximum 150 ha; Gouvernement du Québec 2015). Cut-block width varies from 316m (minimum site width) to 1000m, implying that in the largest blocks, vegetative reproduction and long-distance seeding from intolerant hardwood species may have a reproductive advantage over short-distance seeding species due to distance from seeding source (effective and maximum seeding distance ranges respectively from 20-50m to 100-200m for conifer species and from 100-1000m to 200-5000m for hardwood species).

3.4.2.3. Scenarios

Both forest succession and BDA extensions were used in all simulations, but species abundance and outbreak severity varied between simulation runs due to stochasticity in the various simulated processes. Three forest management scenarios were simulated, based on different composition manipulation strategies: 1) unmanaged; 2) increased hardwood (emulating strong competing vegetation establishment within black spruce plantation; post-harvesting stands composed of 25% white birch, 25% trembling aspen, 25% balsam fir, and 25% black spruce over 80% of harvested area), and 3) increased spruce (black spruce plantation over 100% of harvested area). While the selected scenarios address real management strategies, they represent extreme composition manipulation scenarios which are unrealistic in an operational manner, but will help in evaluating the potential impact of a uniformly increased abundance of hardwoods and minor hosts.

No salvage harvesting treatments were simulated in the model. A site affected by SBW-caused cohort mortality might have harvesting delayed due to a reduced mean cohort age (see *Disturbance Regimes*) and a site affected substantially more than the average, such as pure balsam fir stands, could potentially avoid harvesting for some time (and consequently spruce or hardwood plantation will also be delayed). Competitive species are allowed to establish in plantations in the time steps following plantation establishment only if light requirements are met, if establishment probabilities allow it and if the site has not reached its maximum biomass.

3.4.2.4. Analysis

Total simulation time was set at 200 years and the probabilistic determination of time interval between outbreaks allows outbreak to occur on very short intervals (< 20 years) due to a mean interval of 28 years with a 13-year standard deviation. Thus, to allow enough time for regeneration to establish and grow between outbreaks and to focus on typical cases of SBW dynamics where three outbreaks occur in a balsam fir tree lifetime (seedlings exposed to light by a first outbreak, avoiding the second outbreak due to a young age, and dying in the third outbreak due to a mature stage (Baskerville 1975a)), we selected sites having undergone three successive outbreaks occurring at intervals ≥20 years (see sample site selection procedure; Fig. 3.5). Thus, all subsequent analyses were conducted on a restricted set of sample sites, each having undergone 3 successive outbreaks, hereon defined as "outbreak series". We used these specific time series in order to focus and better describe large-scale SBW-driven successional dynamics.

To generate a sufficient number of sample sites, we ran 30 simulations (or replicates) for the unmanaged scenario. To allow for the entire landbase to be harvested at least once under the two managed scenarios (i.e. no site selection before simulation year 70), we ran 40 simulations for the increased hardwood and increased spruce scenarios due to the more restrictive sample site selection procedure. We thus selected a total of 54 outbreak series of three successive outbreaks: 20 for the unmanaged, 19 for the increased hardwood, and 15 for the increased spruce management scenarios (Table 3.2). Mean time interval between outbreaks ranged from 29 to 33 years and total outbreak series length ranged between 43 and 92 years. The total number of selected sample sites summed to over 655 000 for the unmanaged scenario, 610 000 for the increased hardwood scenario, and 488 000 sites for the increased spruce scenario.

Tableau 3.2. Summary statistics of sample outbreak series and sample sites for the three management scenarios (unmanaged, increased hardwood (plantation of 25% white birch, 25% aspen, 25% balsam fir, and 25% black spruce over 80% of the harvested area), and increased spruce (all harvested area being planted in black spruce)).

Statistics (min. and max. values in parentheses)	**Management scenarios**		
	Unmanaged	Increased Hardwood	Increased spruce
Number of simulation replicates	30	40	40
Number of sample outbreak series	20	19	15
Mean outbreak series length (years)	61 (43, 88)	65 (45, 92)	58 (46, 72)
Mean time interval between outbreaks	31 (20, 59)	33 (20, 55)	29 (20, 45)
Total number of selected sample sites	655 343	610 214	488 129

Notes: Total simulation time was 200 years, but for the analyses we only kept series of three successive outbreaks which occurred at an interval ≥ 20 years (i.e. the sample outbreak series). Simulation year 1 corresponds to 2006, year of the last forest inventory in the study area.

Selected sample sites were classified according to their initial composition (stand type) at the beginning of the outbreak series: balsam fir-dominated host stands (≥75% of site biomass in SBW host species, fir ≥ spruce), black spruce-dominated host stands (≥75% of site biomass in host species, spruce > fir), host-hardwood (≥50% host species, ≥25% hardwood), hardwood-host (≥50% hardwood, ≥25% host), and other stand types (≥25% non-host softwoods or hardwood stands). In the unmanaged scenario, sample sites at the beginning of the outbreak series were relatively well distributed between the 5 stand types, with 16%, 24%, 12%, 10%, and 38% of total sample sites for balsam fir-dominated host stands, black spruce-dominated host stands, host-hardwood, hardwood-host, and other stand types, respectively (Fig. 3.4a). 83% of total sites managed under the increased hardwood scenario had a hardwood-host composition after one forest rotation (i.e. beginning of the outbreak series) (Fig. 3.4b). The increased spruce scenario had 65% of total sample sites in black spruce-dominated host stands after one forest rotation, with also a higher abundance of host-hardwood stands than in the unmanaged scenario (21% vs. 12% of total sample sites, respectively) (Fig. 3.4c). Balsam fir-dominated host stands were less frequent under the increased spruce and increased hardwood scenarios (1% of total sample sites), but still had substantial sample sites totals, with 6 309 and 4 399 sample sites, respectively.

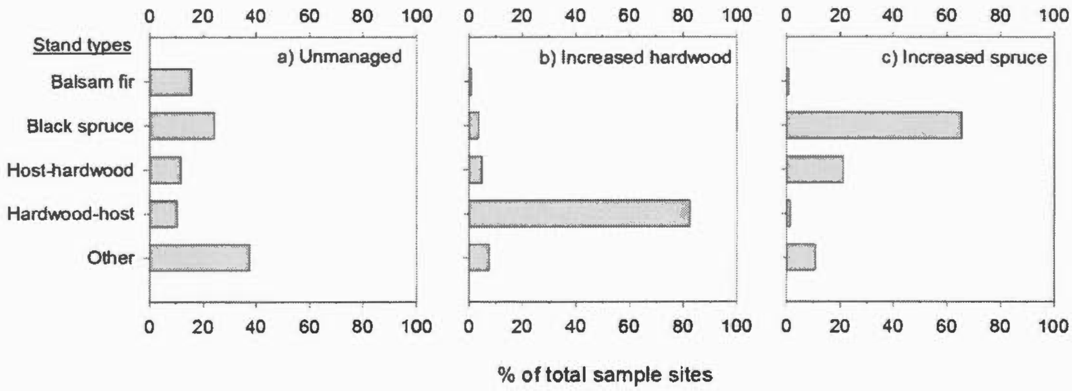

Figure 3.4. Total sample sites per stand type (balsam fir-dominated host stands (≥75% host in total biomass, fir > spruce), black spruce-dominated host stands (≥75% host in total biomass, spruce > fir), host-hardwood (≥50% host spp. and ≥25% hardwoods), hardwood-host stands (≥50% hardwoods and ≥25% host spp.), and other stands (stands with non-host softwood content ≥25% and hardwood stands)) given forest management scenario: a) unmanaged, b) increased hardwood, and c) increased spruce at the beginning of the series of three successive outbreaks (after one 70-year forest rotation for managed scenarios, see Methods).

In each stand type, the percentage of softwood biomass reduction due to cohort mortality per outbreak was estimated for each sample site (Fig. 3.5). These percentages were then classified into mortality classes per outbreak (light: <33% biomass reduction; moderate: 33%-66%; severe: ≥67%) and cumulative mortality classes (light mortality only, at most one moderate or severe mortality event, and at least two moderate or severe mortality events).

The effectiveness of forest management scenarios in reducing SBW-caused mortality was evaluated based on their ability to 1) reduce average biomass reduction due to SBW-caused mortality, 2) reduce cumulative mortality class in the three successive outbreaks (light mortality only, two light mortality events + one moderate to severe mortality event, and at least two moderate to severe mortality events), and 3) reduce the likelihood of severe mortality events. Likelihood of moderate/severe mortality for each stand type was estimated as a function of the number of previous successive light mortality events and used as an indicator of outbreak severity variability for the selected outbreak series, i.e. the steeper the increase in likelihood of severe mortality, the higher variability in mortality levels in consecutive outbreaks. Likelihood of mortality for a given severity sequence is based on the relative abundance of sample sites which underwent one of three specific sequences: 1) moderate/severe–any–any, 2) light–moderate/severe–any, 3) light–light–moderate/severe. The likelihood of moderate/severe mortality after sequence 1 represents the number of sample sites which had a moderate/severe mortality event followed by any severity in the 2nd and 3rd outbreak, divided by all sample sites (Equation 1). The likelihood of moderate/severe mortality after sequence 2 represents the number of sample sites which had a light mortality event followed by a moderate/severe mortality event, then any mortality in the 3rd outbreak, divided by all sample sites which first had a light mortality event (Equation 2). The likelihood of moderate/severe mortality after sequence 3 represents the number of sample sites which had a light severity event followed by another light mortality event, then a moderate/severe mortality event in the 3rd outbreak, divided by all sample sites which had light mortality events in the 1st and 2nd outbreaks (Equation 3).

$$likelihood\ sequence\ 1 = \frac{no.\ sample\ sites_{(moderate/severe-any-any)}}{no.\ sample\ sites_{(any-any-any)}} \quad \text{(Equation 1)}$$

$$likelihood\ sequence\ 2 = \frac{no.\ sample\ sites_{(light-moderate/severe-any)}}{no.\ sample\ sites_{(light-any-any)}} \quad \text{(Equation 2)}$$

$$likelihood\ sequence\ 3 = \frac{no.\ sample\ sites_{(light-light-moderate/severe)}}{no.\ sample\ sites_{(light-light-any)}} \quad \text{(Equation 3)}$$

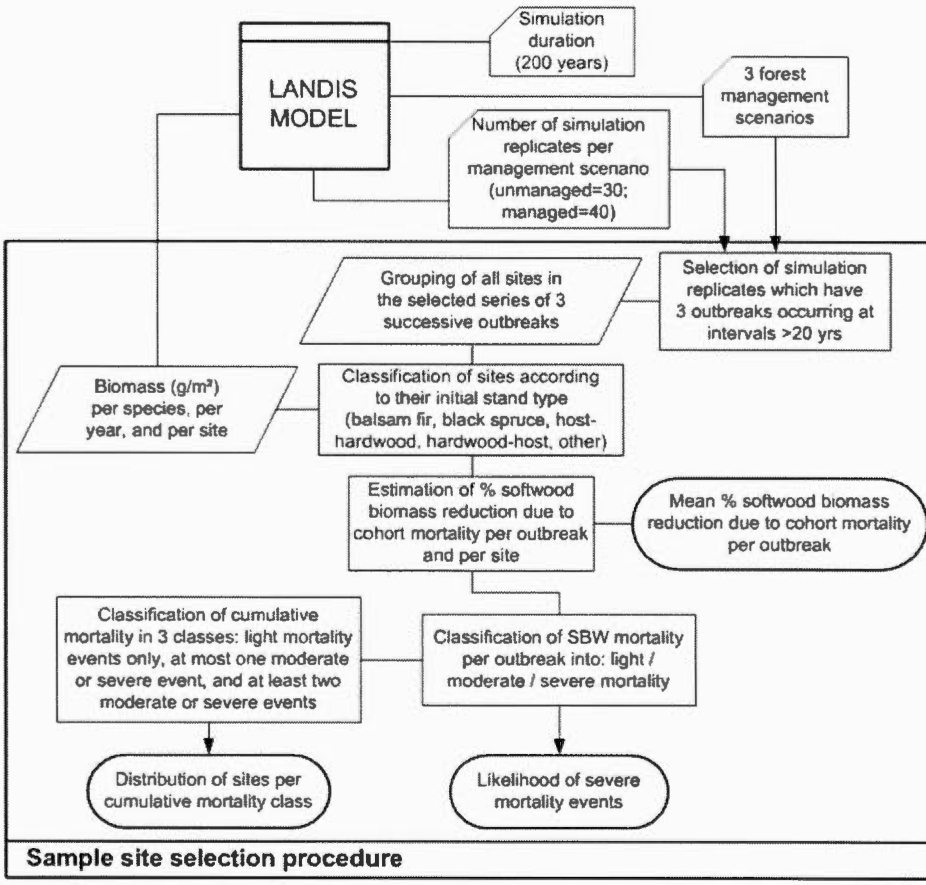

Figure 3.5. Flowchart describing the sample site selection procedure using LANDIS outputted biomass per species and sites (i.e. 10-ha stands) for each of the forest management scenario simulation replicates (unmanaged: 30 replicates, managed scenarios: 40 replicates; see Methods). Sites having undergone three successive outbreaks occurring at intervals ≥20 years were selected to represent typical stand-level SBW dynamics, with two outbreaks occurring in a balsam fir lifetime. Since cohort mortality in the model is probabilistic (based on host species and age), the percentage of softwood biomass reduction for each site due to cohort mortality was estimated for each of the three outbreaks and classified in 3 mortality classes (light, moderate, and severe) and 3 cumulative mortality classes (light mortality events only, at most one moderate or severe event, and at least two moderate or severe events). Based on this information, the

likelihood of severe mortality events and the distribution of sites per cumulative mortality class were estimated.

3.5. RESULTS

3.5.1. Effect of forest management on average and cumulative softwood biomass reduction due to spruce budworm-caused mortality

At the landscape level, despite low mortality even in the unmanaged scenario, the increased spruce scenario was the most effective in decreasing mortality-related biomass reduction with 3% mean softwood biomass reduction due to cohort mortality relative to 5% and 9% for the increased hardwood and unmanaged scenarios, respectively (Fig. 3.6). This effect of forest management scenarios in decreasing mortality was also present for total outbreak series (all three consecutive outbreaks) in the least vulnerable stand types (i.e. mixedwood stands and other stands), with ranges of 4%-6%, 2%-4%, and 7%-8% mean softwood biomass reduction due to cohort mortality for the increased hardwood, increased spruce, and unmanaged scenarios, respectively. There was little difference in mean mortality among scenarios in balsam fir-dominated host stands for total outbreak series (13%, 13%, and 12% mean softwood biomass reduction due to cohort mortality for in the increased hardwood, increased spruce, and unmanaged scenarios, respectively). The increased cohort mortality in balsam fir stands under both managed scenarios relative to the unmanaged scenario was however, more noticeable in the third successive outbreak, with 18%, 16%, and 13% mean softwood biomass reduction due to cohort mortality in the increased hardwood, increased spruce, and unmanaged scenarios, respectively.

Softwood cohort mortality in the unmanaged scenario modestly increased by 3-5% from the first to last outbreak for all stand types (Fig. 3.6a). Both managed scenarios reduced and stabilized softwood biomass reductions relative to the unmanaged scenario in all but the most vulnerable balsam fir stands, with changes ranging -1%–4% biomass reduction from the first to last outbreak.

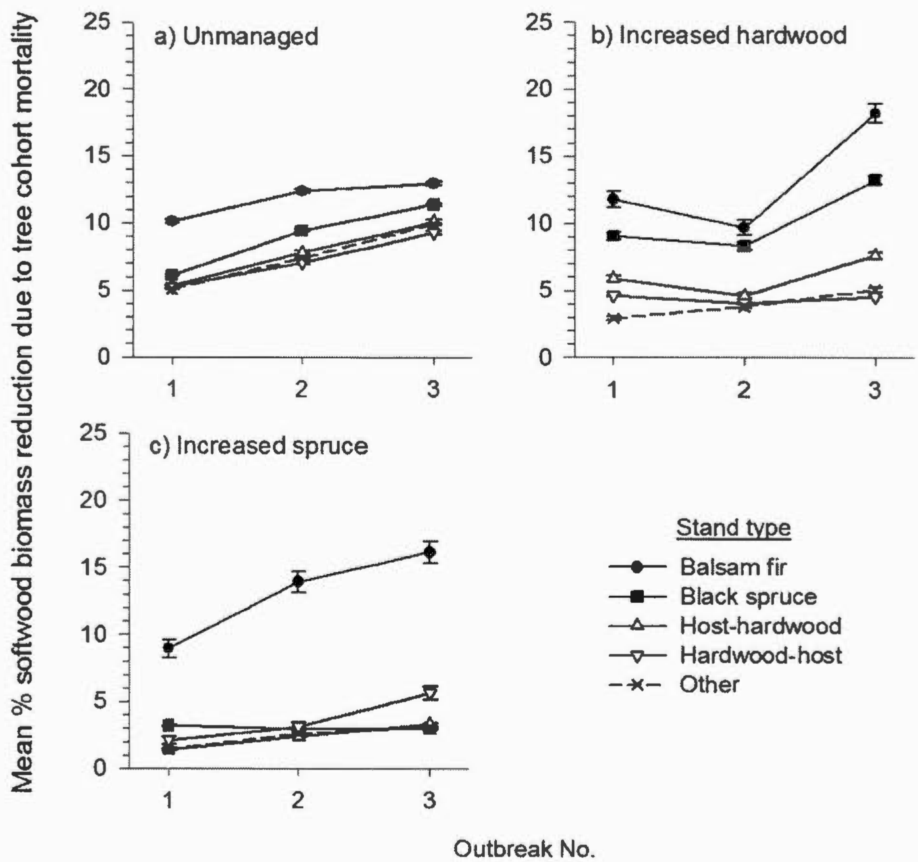

Figure 3.6. Mean softwood biomass reductions due to spruce budworm-caused tree cohort mortality per stand type (balsam fir-dominated host stands, black spruce-dominated host stands, host-hardwood, hardwood-host, and other stands) as a function of outbreak number and given forest management scenario: a) unmanaged, b) increased hardwood, and c) increased softwood. Error bars represent 95% confidence intervals.

The majority of sample sites underwent only light mortality events in all scenarios including the unmanaged scenario (56%-73%, 52%-85%, and 53%-92% of total sample sites for the unmanaged, increased hardwood, and increased spruce scenario, respectively) (Fig. 3.7). With the exception of balsam fir stands, both management scenarios reduced the number of severe/moderate mortality events compared to the unmanaged scenario. This was particularly true for the increased spruce scenario which reduced the number of moderate/severe events by half to two thirds compared to the unmanaged scenario (i.e. 10-15% moderate and severe mortality in the black spruce scenario compared to 25-28% in the unmanaged landscape for all stand types except fir). The increased spruce scenario also reduced the number of moderate/severe mortality events by 41-64% over the increased hardwood scenario in all but the fir and hardwood-host stand types.

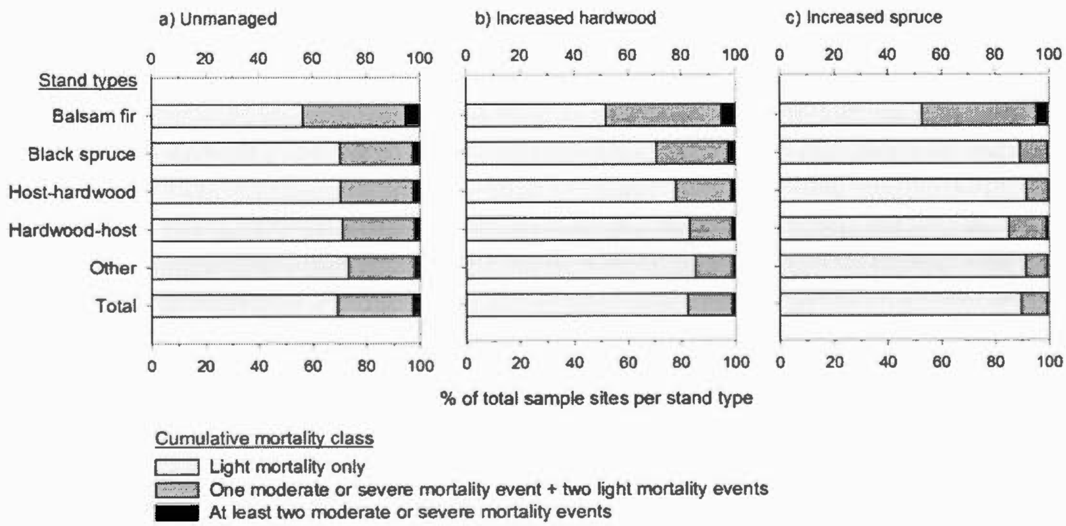

Figure 3.7. Proportion of total sample sites per stand type affected by different cumulative mortality classes for each forest management scenario: a) unmanaged, b) increased hardwood, and c) increased softwood. Mortality classes: light mortality (<33% softwood biomass reduction), moderate mortality (33-66% softwood biomass reduction), and severe mortality (≥67% softwood biomass reduction).

3.5.2. Effect of forest management on the likelihood of severe spruce budworm-caused mortality

We further evaluated the effectiveness of the different management scenarios by estimating the likelihood of moderate/severe mortality occurring for each stand type at the beginning of the outbreak series and after one or two light mortality events. As with the preceding analyses, balsam fir-dominated host stands stood apart from all other stand types in all forest management scenarios, with likelihood of moderate/severe mortality being at least 4% higher than any other stand type (Fig. 3.8). The increased spruce scenario reduced the likelihood of moderate/severe mortality relative to the unmanaged and increased hardwood scenarios for all stand types except balsam fir-dominated host stands (ranging from 2-8%, 4%-13%, and 7-15% for all outbreaks in the increased spruce, increased hardwood and unmanaged scenarios, respectively). However, the increased spruce scenario generated higher likelihood of moderate/severe mortality after two successive light mortality events in balsam fir-dominated host stands relative to the unmanaged scenario, with respectively 27% and 21%. This undesired increase in likelihood of moderate/severe mortality for balsam fir-dominated host stands relative to the unmanaged scenario was accentuated in the increased hardwood scenario, with 32% likelihood after two successive light mortality events (Fig. 3.8b), both managed scenarios having a homogenized and increased host spatial distribution across the study area due to spruce plantation. However, it should be remembered that although the likelihood of moderate or severe mortality increased in these stand types in the managed scenarios, the absolute proportion of these stands in the landscape decreased (Fig. 3.4).

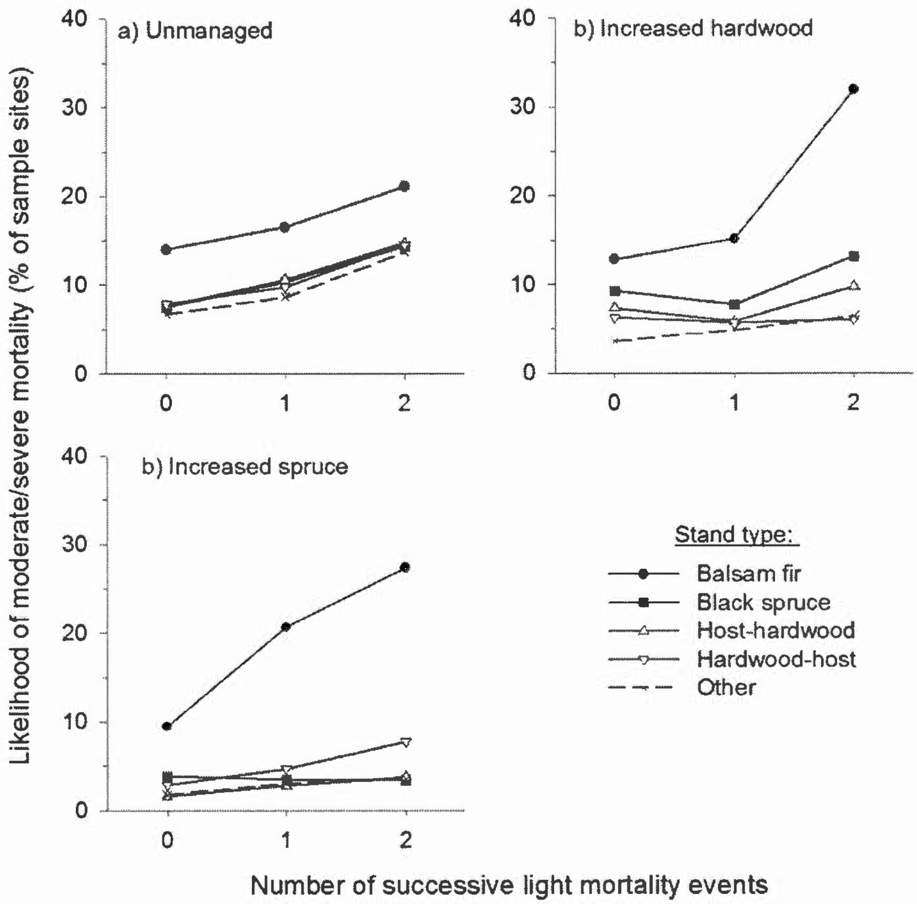

Figure 3.8. Likelihood of moderate/severe mortality events per stand type (balsam fir-dominated host stands, black spruce-dominated host stands, host-hardwood, hardwood-host, and other stands) as a function of the number of successive light mortality events given forest management scenario: a) unmanaged, b) increased hardwood, and c) increased spruce.

3.6. DISCUSSION

3.6.1. Long-term effectiveness of forest management in reducing SBW damage

Stand-level evidence that forest composition influences forest vulnerability to SBW outbreaks (Bergeron et al. 1995; Su et al. 1996) have been at the basis of discussions on the use of silviculture to manipulate forest composition and reduce vulnerability to outbreaks, as opposed to inadvertently increasing vulnerability through increased proportion of balsam fir following traditional harvesting (Blais 1983). Although reducing host species composition is a well-recognised component of a forest protection strategy against insect pests, large-scale conversion of composition to mixed stands and to spruce plantation have begun even though the scientific merit of gains from the presence of other species at the landscape scale is not clear (Miller and Rusnock 1993; Sainte-Marie et al. 2015). For example, it remains uncertain whether the increased protective effect of hardwoods will compensate for softwood volume lost to an increased proportion of hardwood vs. conifer stems in the landscape. Our current study informs the debate by showing that an overall silvicultural effect was obtained over successive, simulated outbreaks with the notable exception of balsam fir-dominated host stands. In the study area, forest management and especially the increased spruce scenario was effective in reducing the overall projected mean and cumulative biomass reductions from mortality and the variability in severity of successive mortality events (i.e. likelihood of moderate/severe mortality).

Given our forested landscape, we did not get strong evidence of SBW-caused mortality varying as a result of mortality levels in previous outbreaks, with the exception of a substantial increase in the likelihood of moderate/severe outbreaks following successive light outbreaks in balsam fir-dominated host stands (Fig. 3.6b-c). Our results also suggest that most stands will undergo light outbreaks, consistent with observations from other mixedwood forested regions, suggesting that SBW outbreaks are a patchy disturbance (Kneeshaw and Bergeron 1998; Chabot et al. 2014). In a forested area to the west of our study area, Bergeron et al. (1995) noted that average mortality across the forested landscape during the 1970-1987 outbreak was 56% and that it varied greatly with stand type, tree size class and site type. However, because we modeled SBW outbreaks to occur synchronously across the landscape, we did not simulate the effect of small outbreak patches, which might be more common in diverse landscapes, promoting more frequent, but less severe outbreaks (Cooke et al. 2007). Furthermore, in our model, stand-level mortality occurred on entire cohorts instead. Nonetheless, our results at the landscape scale showing mostly light mortality suggest a similar patchy mortality.

Long-term forest management succeeded in reducing and stabilizing simulated SBW-related mortality for the least vulnerable stand types, but efforts were ineffective to modify forest vulnerability within a portion of balsam fir-dominated host stands (Fig. 3.7). Holling and Meffe (1996) suggested that this is a common consequence of the command and control approach. However, despite maintaining (or in some cases increasing) the vulnerability of balsam fir stand, both simulated management scenarios reduced balsam fir stand abundance across the landscape so that increased outbreak effects were concentrated in a smaller portion of the landscape. Analyses of more fir-dominated forests and of longer series of successive outbreaks will be required to understand the interaction of landscape context and management practice and to answer the question of whether these management techniques should be of concern within landscapes dominated by balsam fir.

Although the increased spruce scenario seemed to provide the most promising results, caution should be kept in mind as in this exercise, we applied black spruce plantations across the entire landscape, which may be unrealistic on large territories or public lands (but see Black Brook District (Hennigar and MacLean 2010)). Furthermore, plantations in fir- or intolerant hardwood-dominated landscapes are likely to develop into mixed stands (Sainte-Marie et al. *In prep.*– Chapter II in this thesis) without intensive silvicultural tending to maintain the planted species (Pitt and Bell 2005; Sainte-Marie et al. 2015). Global changes may also influence current host species vulnerabilities with warmer springs leading to greater phenological synchrony of the SBW and black spruce (Neau 2014) and thus increased vulnerability (Pureswaran et al. 2015). Such uncertainty suggests that a diversity of approaches may be more appropriate than any one single approach, which is basically what has been done in Quebec for the last decades (Gouvernement du Québec 2009; Sainte-Marie et al. 2015) although not necessarily intentionally. A balanced management approach, promoting both hardwoods and spruce plantations to reduce losses to SBW outbreaks is perhaps the most precautionary approach, in balancing needs for softwood timber, reduced SBW outbreak damage, limited investments in silviculture and long-term stability in forest dynamics. Our results also suggest that caution should be used when extrapolating short-term or small-scale patterns to larger temporal and spatial scales, as new patterns may emerge and potentially increase uncertainty in long-term timber yield projections.

3.7. ACKNOWLEDGEMENTS

Financial support for this research was provided by the Fonds de Recherche Québécois sur la Nature et les Technologies (FRQNT), the Center for Forest Research (CFR) and by the Spray Efficacy Research Group (SERG). We thank Brian Miranda and Eric Beaulieu for technical assistance, Louis Morneau and Cédric Fournier at the Québec ministry of forest, fauna and parks, as well as Elizabeth Campbell at the Canadian Forest Service for data sharing.

CONCLUSION GÉNÉRALE

Retour sur les objectifs

Cette thèse a permis de mettre en lumière différents aspects méconnus sur les conséquences des méthodes sylvicoles préventives de lutte contre la TBE et ce, en laissant quelques surprises au passage. Les lignes qui suivent en résument les principaux points.

À court terme, soit à l'échelle d'une seule épidémie, l'aménagement intensif basé sur l'épinette suivi d'un contrôle de la végétation compétitrice s'est avéré efficace à diminuer la vulnérabilité des forêts et à augmenter le rendement résineux après épidémie. Toutefois, la majorité de l'aménagement intensif utilisé jusqu'à ce jour s'est avéré peu efficace à limiter la végétation compétitrice dans les régions dominées par le sapin, si bien que dans ces régions, l'aménagement préventif n'a pas pu modifier la vulnérabilité des forêts actuelles par rapport à celle prévalant avant la dernière épidémie. Bien entendu, la stratégie québécoise de protection des forêts visait plusieurs objectifs, dont ceux de favoriser la biodiversité et les usages forestiers non-ligneux, mais elle visait avant tout à augmenter la résistance des forêts face aux épidémies d'insectes et à instituer une stratégie de coupe basée sur la régénération naturelle et la gestion de la végétation compétitrice de façon écologique, sans avoir usage de pesticide ou phytocide chimique (Gouvernement du Québec 2000). Bien qu'à certains égards ces objectifs ont été atteint (Gouvernement du Québec 2000), fort est de constater que la stratégie semble avoir essentiellement contribué à limiter les dommages (TBE et végétation compétitrice) davantage qu'à les réduire. À long terme par contre, l'aménagement intensif associé à un contrôle de la végétation s'est avéré efficace à réduire la fréquence, la sévérité et la variabilité de la sévérité des épidémies, mais seulement pour les peuplements les moins vulnérables, soit ceux ayant été traités ou naturellement faibles en sapin. Or, les peuplements les plus vulnérables, soit ceux n'ayant pas été traités, ont vu l'aménagement préventif y maintenir la fréquence d'épidémie, augmenter la sévérité et la probabilité d'épidémies sévères, en augmentant la distribution spatiale des hôtes.

L'aménagement extensif apparaît particulièrement peu efficace à maintenir le rendement résineux à court terme dans les régions dominées par le sapin, et il est apparu que l'effet de protection des feuillus n'est possiblement pas suffisant dans ces régions pour qu'un aménagement qui maintient les feuillus génère un aussi bon rendement résineux après épidémie que l'aménagement intensif orienté vers l'épinette. Or, nos résultats montrent que l'important enfeuillement généré dans cette région était probablement localisé et temporaire, dû à la prédominance du modèle successionnel alternant entre dominance mixte et sapin dans cette région dominée par le sapin baumier avant la dernière épidémie de TBE. À long terme, l'aménagement extensif limiterait les dommages liés à la TBE de manière importante, bien qu'un peu moins que l'aménagement intensif favorisant l'épinette.

Par ailleurs, la composition régionale s'est avérée un facteur important pour prédire la succession après perturbation, qui est apparue très similaire tant après coupe qu'après TBE. L'aménagement extensif ne serait donc pas la principale cause d'enfeuillement depuis la dernière épidémie, allant jusqu'à améliorer le rendement résineux après coupe dans les régions à forte proportion de feuillus. Le modèle de dominance alternée mixte-sapin s'appliquerait donc également à l'aménagement extensif, bien que globalement, la TBE ou la combinaison de la TBE et l'aménagement soient demeurés les principales causes d'enfeuillement en sapinière depuis la dernière épidémie.

Tous les sous-objectifs de cette thèse font appel aux bases de données de SIFORT et au réseau de placettes permanentes du ministère des ressources naturelles, de la faune et des parcs. Ces sources de données sont très informatives afin de suivre l'évolution de la forêt, mais elles comportent également certaines sources d'erreurs à prendre en compte. Par exemple, la base de données SIFORT étant géolocalisée, un décalage est possible entre les inventaires, pouvant causer des incohérences d'un inventaire à l'autre. Or, cette source d'erreur aléatoire et constante dans le territoire se limiterait à 4% des tesselles trouvées en forêt publique et est fortement tempérée à grande échelle, comme celle de la région (Gouvernement du Québec 2015). Nous nous sommes assurés, toutefois, d'utiliser plus d'une source de données pour corroborer nos résultats, comme l'utilisation d'un inventaire terrain comme celui des placettes permanentes en guise de validation (voir chapitre 1). Par ailleurs, tant pour SIFORT que pour les placettes permanentes, la période de référence pour étudier la succession forestière apparaît relativement courte (20-30 ans) par rapport à la dynamique successionnelle en forêt boréale qui implique des cycles s'étendant souvent sur plusieurs cohortes (>200 ans). Or, la période de 20-30 ans utilisée ici est cohérente avec le cycle d'épidémie de la TBE généralement observé au Québec (25-38 ans lors du 20^{e} siècle; Jardon et al. (2003)) et est suffisante pour distinguer la composition des peuplements immatures. Bien-entendu, cette composition est sujette à se modifier d'ici à la maturation des peuplements, mais elle n'en demeure pas moins très informative pour établir le succès de régénération en espèces désirées vs. compétitrices, soit un des concepts-clés de cette thèse.

L'ensemble de cette thèse a donc exposé les forces, mais également les faiblesses de la sylviculture préventive. Elle a montré que malgré des investissements peu efficaces dans l'aménagement intensif jusqu'à présent, le potentiel de cette stratégie est important lorsqu'on limite la végétation compétitrice. L'aménagement extensif, en permettant le maintien de feuillus après coupe, s'est également avéré efficace dans l'ensemble pour réduire la vulnérabilité des forêts, mais son efficacité à augmenter le rendement résineux après épidémie dépendrait largement de la composition avant coupe. De même, l'efficacité de l'approche sylvicole préventive diminuerait grandement lorsqu'elle brise l'isolement des peuplements les plus vulnérables dans le paysage, allant jusqu'à augmenter leur vulnérabilité. Cette thèse montre donc que l'approche préventive s'avère globalement efficace, mais que le contexte local et régional doit être tenu en compte et que cet aménagement doit, par conséquent, être utilisé avec précaution. Une modification radicale de composition à grande échelle, visant à générer des rétroactions négatives en termes de dommages liés aux épidémies d'insectes, modifierait inévitablement la dynamique d'épidémie et pourrait en fait générer des rétroactions positives en termes de dommages, tel que décrit par Holling et Meffe (1996) en tant que phénomène de *Command and control* et tel que vu dans certains aspects de nos simulations à long terme. Il apparaît toutefois peu probable qu'un programme de plantation aussi radical soit faisable à l'échelle d'un territoire aussi grand que la sapinière du Québec, essentiellement pour une question de coût.

Pistes de recherches futures

Puisque plusieurs aspects de la dynamique des épidémies de TBE demeurent méconnus, tel que la dispersion des populations de TBE et de leurs ennemis naturels, de même que les mécanismes climatiques et biologiques régissant l'explosion et le maintien des populations de TBE, nos simulations ont été paramétrées à partir de données empiriques illustrant la dynamique d'épidémies passées. Or, cette dynamique passée risque de se modifier advenant des changements environnementaux liés au climat (Régnière et al. 2012; Pureswaran et al. 2015) ou à l'aménagement (Anderson et al. 1987; Roland et al. 1997). Des recherches sur la dynamique des populations de TBE sont actuellement en cours afin d'approfondir nos connaissances sur la dispersion de la TBE et de ses ennemis naturels, de même que sur les facteurs en cause dans le déclenchement des épidémies. Toutefois, d'ici à ce que des réponses soient disponibles sur ces questions, les relations empiriques demeureront utiles pour planifier l'aménagement forestier en fonction des projections de croissance et des dommages éventuels de la TBE, à condition bien-entendu d'en reconnaître les limites et incertitudes.

Dans cette thèse nous avons utilisé une approche descendante (ou top-down) en assignant une dynamique d'épidémie synchrone à travers le paysage, compte tenu de l'absence de donnée spatiale à petite échelle décrivant la dynamique de contagion des épidémies de TBE et en considérant le rayon de dispersion de la TBE potentiellement assez grand (>150 km)

(Sturtevant et al. 2013). Afin d'adopter une approche davantage ascendante (ou bottom-up) permettant l'émergence de patrons à grande échelle à partir de paramètres locaux simples, il serait éventuellement possible d'observer les patrons spatiaux de contagion des épidémies de TBE passées afin de déterminer les probabilités de défoliation en fonction des taux de défoliation des peuplements avoisinants. Ces questions ont déjà été traitées pour d'autres ravageurs forestiers (Foster et al. 2013) et pour les épidémies de TBE à très grande échelle (Bouchard et Auger 2014), mais il demeure difficile de prévoir l'évolution de la défoliation à l'échelle du peuplement, échelle de base de la planification forestière, d'où le besoin pour des données plus précises. Une approche ascendante permettrait aussi d'évaluer l'effet de modalités de récolte à petite échelle, telle que la taille de trouée, dont l'impact cumulatif sur le régime d'épidémie a déjà suggéré (Robert et al. 2012).

Les facteurs régissant la succession forestière en sapinière sont également peu connus, les uns observant une succession sapin-sapin dans certains cas et les autres observant un retour accru d'espèces feuillues intolérantes après TBE ou après coupe dans d'autres cas. Dans la présente thèse, nous avons observés les deux cas et avons ciblé la composition avant perturbation comme étant un facteur explicatif important à grande échelle, mais à l'échelle locale, les facteurs déterminants demeurent méconnus. Certains ont suggéré le rôle de facteurs locaux édaphiques et environnementaux associés à la taille des trouées pour expliquer la succession forestière en sapinière (Kneeshaw et Bergeron 1998; Bouchard et al. 2006), mais cette hypothèse n'a pas encore été approfondie. Une analyse terrain à l'échelle du domaine de la sapinière observant le rôle de différents facteurs environnementaux à la base des différents grands patrons successionnels aiderait certainement à approfondir cette question et à informer les aménagistes sur les risques potentiels d'enfeuillement à l'échelle locale.

Finalement, dans cette thèse nous avons observé l'effet à long terme de l'aménagement préventif sur les dommages liés à la TBE, mais une analyse coût-bénéfice ou du moins, une analyse du rendement en bois résineux serait essentielle afin de déterminer la rentabilité de l'aménagement préventif à long terme. L'aménagement intensif apparaît efficace à grande échelle pour limiter les dommages de la TBE, mais l'effet néfaste de connexion des peuplements vulnérables à faible proportion d'aménagement intensif dans le paysage reste inconnu et l'aménagement favorisant les feuillus est également efficace tout en requérant beaucoup moins d'investissement. Compte tenu des budgets généralement limités, une analyse coût-bénéfice permettrait également d'estimer une proportion optimale du territoire à aménager intensivement. Une telle analyse permettrait également d'estimer la rentabilité d'un aménagement uniquement extensif, mais allouant une meilleure régénération résineuse, telle que suggéré par certains (Benson 1988). Il existe également divers enjeux sociaux ou écologiques liés au maintien d'une biodiversité plus grande en forêt (i.e. maintien d'espèces compagnes en forêt boréale aménagée) et autres services écosystémiques et ceux-ci n'en sont pas moins monnayables (De Groot et al. 2012), d'où l'intérêt pour déterminer la valeur des services écosystémiques non-ligneux.

Recommandations d'aménagement forestier

Il nous apparaît important d'évaluer les risques d'enfeuillement dans le processus de planification de l'aménagement forestier en forêt boréale mixte. Nos résultats suggèrent qu'un enfeuillement est possible dans l'ensemble de la sapinière du Québec, mais que les forêts à dominance résineuse en sont plus susceptibles. Considérant les risques d'enfeuillement en sapinière, il nous apparaît important d'approfondir cet aspect de la succession encore méconnu qui s'appliquerait autant aux sites affectés par la TBE que ceux aménagés extensivement. Suivant cette logique, dans les secteurs sensibles à l'enfeuillement, il serait éventuellement possible de planifier des coupes favorisant la rétention d'épinettes semencières et limitant la taille des blocs de coupe.

Selon nos résultats, l'aménagement intensif d'épinette, tel qu'utilisé actuellement en sapinière, n'a clairement pas les effets souhaités compte tenu de l'envahissement par la végétation compétitrice et ne rapportera probablement pas les bénéfices escomptés. Cette situation a également déjà été observée en Ontario (Benson 1990). Toutefois, Wagner et al. (2006) insiste sur le fait qu'un suivi efficace de la végétation compétitrice doit être effectué pour espérer des gains de rendement. Nos simulations d'aménagement intensif d'épinette à long terme ont montré une grande efficacité à diminuer la vulnérabilité à grande échelle, mais dans ce cas, une gestion de la végétation efficace était essentiellement implicite dans le modèle, compte tenu du faible envahissement par la végétation compétitrice par rapport à ce que nous avons observé au Québec depuis la dernière épidémie.

A la lumière de nos résultats, il faudrait possiblement concentrer les efforts d'aménagement intensif sur un nombre plus restreint de peuplements afin de limiter la végétation compétitrice, potentiellement où les gains seraient les meilleurs, donc dans les secteurs les plus productifs. Il a aussi été suggéré que les ressources monétaires allouées à la petite proportion du territoire aménagé intensivement (<20% du territoire aménagé total au Québec) soient plutôt utilisées pour l'aménagement extensif, de manière à planifier des récoltes assurant une meilleure régénération résineuse sur tout le territoire aménagé extensivement (Benson 1990). Bien que l'idée apparaisse justifiable, il nous est difficile de se prononcer sur ce débat sans une analyse coût-bénéfice en bonne et due forme, qui intégrerait bien-entendu tant l'effet positif que négatif associé aux feuillus dans les sapinières.

Compte tenu des risques inhérents à chaque approche d'aménagement préventif, une diversité de traitements semble encore la meilleure option pour balancer ces risques et limiter l'incertitude liée à l'aménagement. Ceci inclut nécessairement les approches d'aménagement réactif peut-être plus coûteuses, mais dont l'efficacité est démontrée, tel que l'épandage d'insecticide, ou des approches plus « hybrides » telles que la pré-récupération des peuplements vulnérables à la TBE avant l'apparition des dommages ou la récolte prioritaire basée sur une classification de la vulnérabilité. Il est à noter que ces formes de récupération préventive engendre un certain coût indirect lié au fait que ces peuplements seront possiblement récoltés avant un âge optimal, se privant donc d'un volume potentiel non-négligeable (Hennigar et al. 2007). Si l'on considère une approche plus efficace d'aménagement intensif, donc sur un nombre plus restreint de sites, il en ressort que l'aménagement tel que pratiqué actuellement, avec sa diversité de traitements ayant des avantages différents et complémentaires, n'est pas si mauvais en soi d'un point de vue général. Par contre, les prévisions de rendement demeurent non-explicites sur les points des pertes de rendement liées à la TBE et à l'enfeuillement après coupe, augmentant ainsi les risques de surexploitation de la ressource forestière. Ces aspects, parallèlement à la redéfinition des traitements sylvicoles pour optimiser la quantité de feuillus et augmenter leur efficacité, constituent sans aucun doute les principales recommandations à tirer de cette thèse.

APPENDICE A

Sensitivity analysis of pre-outbreak timber yield estimates (Chapter 1)

A limitation of our approach used in Chapter 1 is that there is a potential bias associated with yield estimations based on a small number of field observations (i.e. insufficient number of sampled stands for a given yield estimate). However, using yield estimates based on the same volume growth data in the pre- and post-outbreak inventory generated a constant bias between the two inventories, allowing for reliable comparisons of pre- and post-outbreak yield estimates.

To assess species composition at the time of the pre- and post-outbreak inventories for each of the five stand types (used in the 3 study regions described in Chapter 2), we used local permanent sample plots (PSP) within 50 km of study regions, for a total of 94, 330, and 183 plots for the hardwood-, black spruce-, and balsam fir-dominated regions, respectively. To assess potential bias in the pre-outbreak timber yield estimates, we first evaluated the variability in the PSPs species proportions for each of the five stand types between the two inventories. Species proportions in the PSPs differed by an average of 6.0% ± 3.5% (std. dev.) of total stems per stand type between the pre- and post-outbreak inventories and softwood/hardwood proportions differed by a maximum of 12% of total stems. The largest changes in species proportions between the two inventories were found with spruce species and other softwoods (mostly jack pine, but also eastern cedar and tamarack), ranging respectively from -9% to 27% and -21% to 7%. Because these changes were substantial, we evaluated whether a substitution in the most common softwood species (balsam fir, spruce species, other softwoods) between the pre- and post-outbreak inventories would affect stand softwood yield given the proportion in total stand yield and the location along the longitudinal gradient covered by the three landbases. However, relationships between species proportion of total stand yield and merchantable volume yield (for 70 years old stands) remained similar for all softwood species found in the three study regions (described in Chapter 2), suggesting a constant softwood yield independently of softwood species composition.

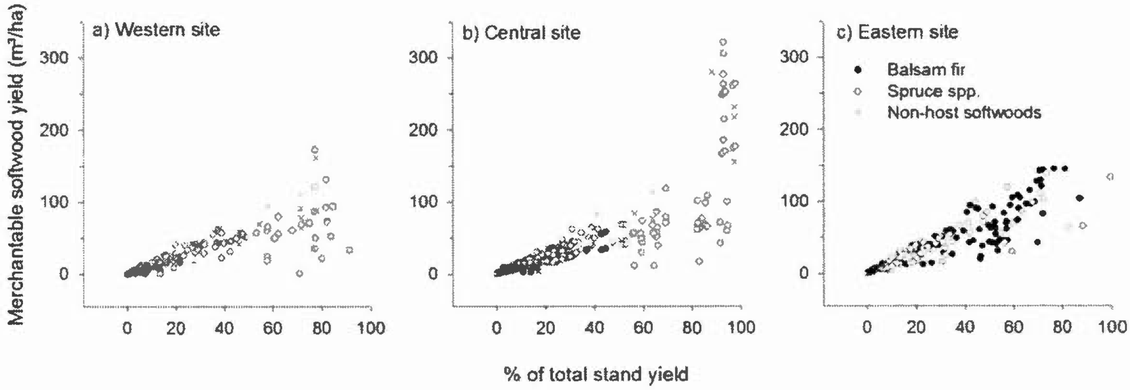

Figure 3.9. Merchantable volume yield for softwood species (balsam fir, spruce species, and non-host softwoods) within 70-year-old stands for the three study regions (Chapter 1: Eastern site only) as a function of species proportion in the stand.

APPENDICE B

Site disturbance probability and determination of cohort mortality (Chapter 3)

Equation 1 describes how site disturbance probability (SDP) is determined in the Biological Disturbance Agent (BDA), based on site- and landscape-level species composition and age, along with the ROS (regional outbreak status), a parameter equivalent to regional budworm population level and set to vary from 1 (low population level) to 3 (high population level) in our model. Determination of SDP is among the last steps before cohort mortality actually occurs in the model. If SDP is <33%, a light outbreak will be generated, if SDP is between 33-66%, a moderate outbreak will be generated and if SDP is >66%, a severe outbreak will be generated. Then, a random number is generated and compared with probabilities of cohort mortality (Table 3.1) and cohorts present on a given site will be killed if that number is below their probability of mortality.

$$Site\ disturbance\ probability = a \cdot \left\{\left(SSV + \frac{NSV \times NW}{1+NW}\right)\right\} \cdot \frac{ROS}{3} \qquad \textbf{(Equation 1)}$$

Where a is a used-defined calibration parameter ($a = 1$ in this case); SSV = site susceptibility value, based on the average value of the oldest cohort of each tree species per site (range 0-1); NSR = neighborhood susceptibility value (range 0-1); NW = neighborhood weight, a parameter defining the relative importance between site and neighborhood resources (range 0.01-100); ROS = regional defoliation severity (range 1-3).

Relative effect of site vs. neighborhood hardwood content on biomass reductions (Chapter 3)

The BDA model allows users to specify the relative weight given to site and landscape-level composition on susceptibility to the SBW and considering that dispersal of natural enemies of the SBW is still not well understood (Cooke et al. 2007), a sensitivity analysis was conducted assigning in one case a dominant landscape weight (90% landscape, 10% site) to site susceptibility value to assess the impact of higher natural enemy dispersal (Roland and Taylor 1997) and in the other case a dominant site weight (90% site, 10% landscape) was assigned to assess the impact of lower natural enemy dispersal.

We found different patterns of hardwood content effect on softwood biomass reductions and strong influences of management types, outbreak sequence, and spatial scale on the size of the hardwood protection effect (Fig. 8). As expected from the lowest hardwood presence in the increased spruce management (Fig. 3), the site-centered hardwood content effect (the default setting in our analyses; 90%/10% site vs. neighborhood hardwood content weight calculation) was lowest under increased spruce management, with 16% mean prevented softwood biomass reduction. Yet, the mean site-centered hardwood content effect was unexpectedly lower in the increased hardwood scenario than in the unmanaged scenario in the first outbreak. This relationship was inverted in the second and third outbreak, where the increased hardwood management scenario had >4% higher prevented softwood biomass reductions relative to the unmanaged scenario.

Effects were similar whether using site-centered or landscape-centered hardwood content for the unmanaged scenario, with a 46%-36% decrease and a 38%-24% decrease in mean prevented biomass reduction between the first and third outbreaks, respectively. Globally, the trends were also similar in the increased hardwood scenario, with a 10%-45% increase and a 31%-54% increase in mean prevented biomass reduction for the site- and landscape-centered hardwood content effect, respectively. This similarity in hardwood content effects thus limits the role of spatial scale in estimating the hardwood content effect on biomass reductions.

However, while site- and landscape-centered effects were different for the increased spruce scenario, hardwoods are much less abundant in this scenario relative to the others (i.e. 15% of total biomass relative to 26% and 54% for the unmanaged and increased hardwood scenarios, respectively), thereby limiting the consequences of this difference in hardwood content effects for the increased spruce scenario.

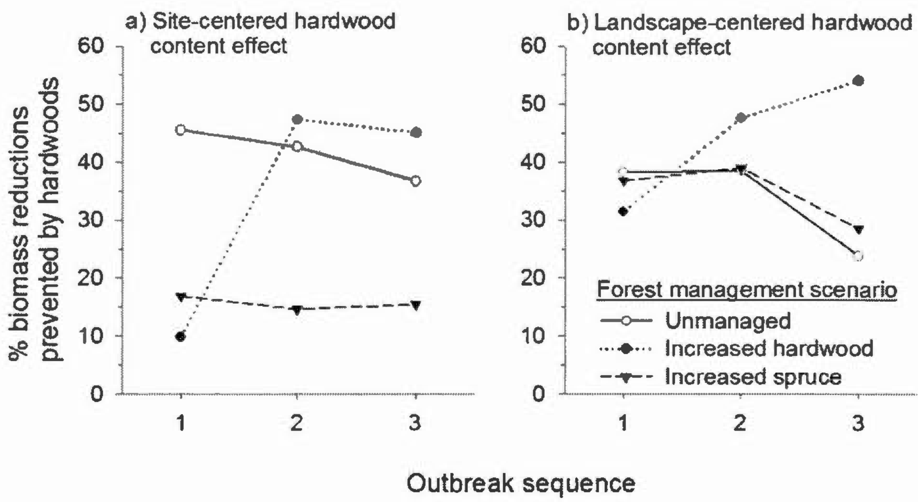

Figure 3.10. Proportion of biomass reductions prevented by hardwoods as a function of outbreak sequence and given forest management scenario (unmanaged, increased hardwood, and increased black spruce), and the inclusion of a) site-centered hardwood content effect (90%/10% site vs. neighborhood hardwood content weight calculation) and b) landscape-centered hardwood content effect (10%/90% site vs. neighborhood hardwood content weight calculation, see Methods). Neighborhood size was set at a 1 km-radius, based on Campbell et al. (2008).

RÉFÉRENCES

Anderson, L., Carlson, C.E., and Wakimoto, R.H. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. For. Ecol. Manage. **22**(3): 251-260.

Barrette, M. 2004. Caractérisation du paysage primitif de la région écologique des hautes collines du bas-saint-maurice pour une gestion des écosystèmes du parc national du canada de la mauricie. *In* Faculté de foresterie et de géomatique. Université Laval, Sainte-Foy, Québec. 137 p.

Baskerville, G.L. 1975a. Spruce budworm: super silviculturist. For. Chron. **51**: 138-140.

Baskerville, G.L. 1975b. Spruce budworm: the answer is forest management: or is it. For. Chron. **51**: 157-160.

Batzer, H.O., Benzie, J.W., and Popp, M.P. 1987. Spruce Budworm Damage in Aspen/Balsam Fir Stands Affected by Cutting Methods. Northern Journal of Applied Forestry **4**(2): 73-75.

Bauce, É. 1996. One and two years impact of commercial thinning on spruce budworm feeding ecology and host tree foliage production and chemistry. For. Chron. **72**(4): 393-398.

Belle-Isle, J., and Kneeshaw, D. 2007. A stand and landscape comparison of the effects of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak to the combined effects of harvesting and thinning on forest structure. For. Ecol. Manage. **246**(2-3): 163-174.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology **81**(6): 1500-1516.

Bergeron, Y., and Archambault, S. 1993. Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the'Little Ice Age'. The Holocene **3**(3): 255-259.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**(3): 384-391.

Bergeron, Y., and Leduc, A. 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern canadian boreal forest. J. Veg. Sci. **9**(4): 493-500.

Bergeron, Y., Leduc, A., Joyal, C., and Morin, H. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. **25**(8): 1375-1384.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. **11**(3): 620-629.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. **13**(4).

Blum, B.M., and MacLean, D.A. 1984. Silviculture, forest management, and the spruce budworm. *In* Spruce budworms handbook: managing the spruce budworm in eastern North America. *Edited by* D.M. Schmidt and D.G. Grimble and J.L. Searcy. USDA Forest Service, Washington, D.C. pp. 83-102.

Bognounou, F., Kneeshaw, D., and De Grandpré, L. In review.

Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology **87**(9): 2319-2329.

Bouchard, M., Kneeshaw, D., and Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. Can. J. For. Res. **37**(4): 763-772.

Boudewyn, P., Song, X., Magnussen, S., and Gillis, M. 2007. Model-based, volume-to-biomass conversion for forested and vegetated land in Canada. Pacific Forestry Centre. BC-X-411.

Boulanger, Y., and Arseneault, D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. Can. J. For. Res **34**: 1035-1043.

Boulanger, Y., Arseneault, D., Morin, H., Jardon, Y., Bertrand, P., and Dagneau, C. 2012. Dendrochronological reconstruction of spruce budworm (Choristoneura fumiferana) outbreaks in southern Quebec for the last 400 years. This article is one of a selection of papers from the 7th International Conference on Disturbance Dynamics in Boreal Forests. Can. J. For. Res. **42**(7): 1264-1276.

Campbell, E.M. 2008. Temporal and spatial patterns in the severity of spruce budworm outbreaks in relation to bioclimatic conditions in eastern Canada. *In* Département des sciences biologiques. Université du Québec à Montréal, Montréal, Québec p.

Campbell, E.M., MacLean, D.A., and Bergeron, Y. 2008. The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. For. Sci. **54**(2): 195-205.

Cappuccino, N., Houle, M.J., and Stein, J. 1999. The influence of understory nectar resources on parasitism of the spruce budworm *Choristoneura fumiferana* in the field. Agric. For. Entomol. **1**(1): 33-36.

Cappuccino, N., Lavertu, D., Bergeron, Y., and Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia **114**(2): 236-242.

Carleton, T.J., and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey in the central Canadian boreal forest. Ecoscience: 141-152.

Chabot, M., Boulet, B., and Morneau, L. 2013. La tordeuse des bourgeons de l'épinette. *In* Le guide sylvicole du Québec, tome 1; Les fondements biologiques de la sylviculture. *Edited by* B. Boulet and M. Huot. Les publications du Québec, Québec. pp. 400-414.

Chabot, M., Jetté, J.-P., Vaillancourt, M.A., Fournier, C., Beaupré, P., and Bouchard, M. 2014. L'aménagement écosystémique dans un contexte d'épidémie de la tordeuse des bourgeons de l'épinette; Guide de référence pour moduler les activités d'aménagement dans les forêts publiques. Ministère des forêts, de la faune et des parcs. Gouvernement du Québec. Direction de l'aménagement et de l'environnement forestiers et Direction de la protection des forêts.

Cooke, B.J., Nealis, V.G., and Regniere, J. 2007. Insect defoliators as periodic disturbances in northern forest ecosystems. *In* Plant disturbance ecology: the process and the response. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press. pp. 487-525.

Coulombe, G., Huot, J., Arseneault, J., Bauce, É., Bernard, J.-T., Bouchard, A., Liboiron, M.-A., and Szaraz, G. 2004. Rapport de la commission d'étude sur la gestion de la forêt publique québécoise. Bibliothèque nationale du Québec p.

Couture, C., Girard, J., and Lacasse, C. 2009. Orientations pour l'élaboration du calcul de possibilités forestières (CPF) pour la période 2013-2018. *Edited by* D.d.c.d.p. forestières. Bureau du forestier en chef, Québec. 24 p.

Cyr, D., Gauthier, S., Bergeron, Y., and Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. **7**(10): 519-524.

De Groot, R., Brander, L., Van Der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossman, N., Ghermandi, A., and Hein, L. 2012. Global estimates of the value of ecosystems and their services in monetary units. Ecosystem services **1**(1): 50-61.

Duchesne, L., and Raulier, F. 2004. Analyse de la méthodologie utilisée pour l'évaluation du calcul de possibilité forestière au Québec. *In* Rapport détaillé du comité scientifique chargé d'examiner le calcul de la possibilité forestière. *Edited by* R. Jobidon and M. Bernier-Cardou and G. Blais and C. Gagné and G. Gauthier and J. Moisan and F. Pelletier and D. Pothier and G. Prégent and F. Raulier and C.-H. Ung and S. Végiard. Ministère des ressources naturelles de la faune et des parcs - Direction de la recherche forestière. pp. 5-49 p.

Erdle, T.A., and MacLean, D.A. 1999. Stand growth model calibration for use in forest pest impact assessment. For. Chron. **75**(1): 141-152.

Etheridge, D.A., MacLean, D.A., Wagner, R.G., and Wilson, J.S. 2005. Changes in landscape composition and stand structure from 1945–2002 on an industrial forest in New Brunswick, Canada. Can. J. For. Res. **35**(8): 1965-1977.

Fall, A., and Fall, J. 2001. A domain-specific language for models of landscape dynamics. Ecol. Model. **141**(1): 1-18.

Fortin, M., and Langevin, L. 2010. ARTEMIS-2009: un modèle de croissance basé sur une approche par tiges individuelles pour les forêts du Québec. Gouvernement du Québec. Ministère des ressources naturelles et de la faune. Direction de la recherche forestière. Mémoire de recherche no.156.

Forus Research. 2010. Forus Simulation Framework user guide. Fredericton, New Brunswick, Canada p.

Gagnon, R., and Chabot, M. 1991. Prévention des pertes de bois attribuables à la tordeuse des bourgeons de l'épinette. Gouvernement du Québec, Ministère des Forêts, Direction des programmes, service d'aménagement forestier.

Gauthier, S., Vaillancourt, M.A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, L., and Paré, D. 2009. Forest Ecosystem Management: Origins and Foundations. *In* Ecosystem management in the boreal forest. *Edited by* S. Gauthier and M.A. Vaillancourt and A. Leduc and L. de Grandpré and D. Kneeshaw and H. Morin and P. Drapeau and Y. Bergeron. Presses de l'Université du Québec.

Gouvernement du Québec. 1998. Mise à jour du régime forestier / Document de référence / Bilan - Enjeux - Orientations. Ministère des ressources naturelles p.

Gouvernement du Québec. 2000. Bilan de l'implantation de la Stratégie de protection des forêts 1995-1999. *Edited by* D.d.p. forestiers. Ministère des ressources naturelles du Québec. 24 p.

Gouvernement du Québec. 2009. Portrait de l'évolution de la forêt publique sous aménagement du Québec méridional des années 1970 aux années 2000. *Edited by* Ministère des Ressources naturelles de la Faune et des Parcs. Direction des inventaires forestiers et Direction de l'environnement et de la protection des forêts. 142 p.

Gouvernement du Québec. 2015. Portrait de la régénération naturelle en forêt publique sous aménagement du Québec méridional des années 1970-2010. *Edited by* Ministère des forêts de la faune et des parcs. Secteur des forêts. Direction des inventaires forestiers. 78 p.

Gray, D.R., Régnière, J., and Boulet, B. 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. For. Ecol. Manage. **127**(1-3): 217-231.

Harvey, B., and Brais, S. 2002. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. Can. J. For. Res. **32**(4): 653-666.

Harvey, B.D., and Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. **19**(11): 1458-1469.

Harvey, B.D., Leduc, A., and Bergeron, Y. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. Can. J. For. Res. **25**(10): 1658-1672.

He, H.S., and Mladenoff, D.J. 1999. The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems **2**(4): 308-319.

Helms, J. 1998. The Dictionary of Forestry. Society of American Foresters, Bethesda, MD.

Hennigar, C.R., and MacLean, D.A. 2010. Spruce budworm and management effects on forest and wood product carbon for an intensively managed forest. Can. J. For. Res. **40**(9): 1736-1750.

Hennigar, C.R., MacLean, D.A., Porter, K.B., and Quiring, D.T. 2007. Optimized harvest planning under alternative foliage-protection scenarios to reduce volume losses to spruce budworm. Can. J. For. Res. **37**(9): 1755-1769.

Hennigar, C.R., MacLean, D.A., Quiring, D.T., and Kershaw, J.A. 2008. Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. For. Sci. **54**: 158-166.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. **4**: 1-23.

Holling, C.S., and Meffe, G.K. 1996. Command and control and the pathology of natural resource management. Conserv. Biol. **10**(2): 328-337.

James, P.M.A., Fortin, M.J., Sturtevant, B.R., Fall, A., and Kneeshaw, D. 2010. Modelling Spatial Interactions Among Fire, Spruce Budworm, and Logging in the Boreal Forest. Ecosystems: 1-16.

James W. Sewall Company. 2011. Spruce-fir resource in the state of Maine. Maine Department of Conservation. Available from http://www.maine.gov/dacf/mfs/archive/pubs/pdf/spruce_fir_resource_rpt.pdf p.

Jardon, Y. 2001. Analyses temporelles et spatiales des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *In* Environmental Sciences Dept. Université du Québec à Montreal, Montreal. 157 p.

Jardon, Y., Morin, H., and Dutilleul, P. 2003. Périodicité et synchronisme des épidemies de la tordeuse des bourgeons de l'épinette au Québec. Can. J. For. Res. **33**(10): 1947-1961.

Kneeshaw, D., Sturtevant, B., Cooke, B., Work, T.T., Pureswaran, D.S., De Grandpré, L., and MacLean, D.A. 2015. Insect Disturbances in Forest Ecosystems. *In* Routledge handbook of forest ecology. *Edited by* K.S.H. Peh and R. Corlett and Y. Bergeron. Routledge, New York, NY.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology **79**(3): 783-794.

Koricheva, J., Vehviläinen, H., Riihimäki, J., Ruohomäki, K., Kaitaniemi, P., and Ranta, H. 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality? Can. J. For. Res. **36**(2): 324-336.

Laflèche, V., Ruel, J.-C., and Archambault, L. 2000. Evaluation de la coupe avec protection de la regeneration et des sols comme methode de regeneration de peuplements melanges du domaine bioclimatique de la sapiniere a bouleau jaune de l'est du Québec, Canada. The Forestry Chronicle **76**(4): 653-663.

Larocque, G.R., Shugart, H.H., Xi, W., and Holm, J.A. 2016. Forest Succession Models. *In* Ecological Forest Management Handbook. Taylor & Francis. p. 179.

MacLean, D.A. 1980. Vulnerability of fir–spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. **56**: 213-221.

MacLean, D.A. 1988. Effects of spruce budworm outbreaks on vegetation, structure, and succession of balsam fir forests on Cape Breton Island, Canada. *In* Plant form and vegetation structure. *Edited by* M.J.A. Werger and P.J.M. van der Aart and H.J. During and J.T.A. Verhoeven. SPB Academic Publishing The Hague, Netherlands. pp. 253–261.

MacLean, D.A. 1996. Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. For. Chron. **72**(4): 399-405.

MacLean, D.A. 2004. Predicting natural forest insect disturbance regimes. *In* Emulating natural forest landscape disturbances: concepts and applications. *Edited by* A.H. Perera and L.J. Buse and M.G. Weber. Columbia University Press, New York. pp. 69–82.

MacLean, D.A., and Andersen, A.R. 2008. Impact of a spruce budworm outbreak in balsam fir and subsequent stand development over a 40-year period. For. Chron. **84**(1): 60-69.

MacLean, D.A., Erdle, T.A., MacKinnon, W.E., Porter, K.B., Beaton, K.P., Cormier, G., Morehouse, S., and Budd, M. 2001. The spruce budworm decision support system: forest protection planning to sustain long-term wood supply. Can. J. For. Res **31**(10): 1742-1757.

MacLean, D.A., and MacKinnon, W.E. 1997. Effects of stand and site characteristics on susceptibility and vulnerability of balsam fir and spruce to spruce budworm in New Brunswick. Can. J. For. Res. **27**(11): 1859-1871.

MacLean, D.A., and Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Can. J. For. Res. **19**(9): 1087-1095.

Marchand, S. 1991. Dynamique de la régénération naturelle de jeunes sapinières boréales du centre du Québec. *In* M.Sc. Thesis. Université Laval, Québec city, Québec. p.

McLeod, I., Lucarotti, C.J., Hennigar, C.R., MacLean, D.A., Holloway, A., Cormier, G., and Davies, D. 2012. Advances in aerial application technologies and decision support for integrated pest management. *In* Integrated pest management and pest control. *Edited by* S. Soloneski and M. Larramendy. InTech Open Access Publisher, Rijeka, Croatia. pp. 651–668.

Miller, A., and Rusnock, P. 1993. The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. For. Ecol. Manage. **61**(1-2): 171-189.

Moreau, G., Eveleigh, E.S., Lucarotti, C.J., and Quiring, D.T. 2006. Stage-specific responses to ecosystem alteration in an eruptive herbivorous insect. J. Appl. Ecol. **43**(1): 28-34.

Morin, H., Jardon, Y., and Gagnon, R. 2007. Relationship between spruce budworm outbreaks and forest dynamics in eastern North America. *In* Plant disturbance ecology: the process and the response. *Edited by* E.A. Johnson and K. Miyanishi. Elsevier, New York. pp. 555–564.

Neau, M. 2014. Synchronisme phénologique d'un insecte herbivore avec ses hôtes face au changement climatique: cas de la tordeuse des bourgeons de l'épinette (Choristoneura fumiferana (Clemens)), M.Sc. Thesis. Université du Québec à Montréal, Montréal, QC. p.

Needham, T., Kershaw, J.A., MacLean, D.A., and Su, Q. 1999. Effects of mixed stand management to reduce impacts of spruce budworm defoliation on balsam fir stand-level growth and yield. Northern Journal of Applied Forestry **16**: 19-24.

Pelletier, G., Dumont, Y., and Bédard, M. 2007. SIFORT: Système d'Information forestière par tesselle. Manuel de l'usager. Ressources naturelles et Faune, Québec.

Pitt, D.G., and Bell, F.W. 2005. Juvenile response to conifer release alternatives on aspen-white spruce boreal mixedwood sites. Part I: Stand structure and composition. The Forestry Chronicle **81**(4): 538-547.

Pothier, D. 2002. Twenty-year results of precommercial thinning in a balsam fir stand. For. Ecol. Manage. **168**(1-3): 177-186.

Pothier, D., Elie, J.G., Auger, I., Mailly, D., and Gaudreault, M. 2012. Spruce budworm-caused mortality to balsam fir and black spruce in pure and mixed conifer stands. For. Sci. **58**(1): 24-33.

Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières québécoises se développant en peuplements purs et réguliers. . Gouvernement du Québec, Ministère des Ressources naturelles du Québec, Direction de la recherche forestière, Sainte-Foy, Québec p.

Power, J.M. 1991. National data on forest pest damage. *In* Canada's timber resources. *Edited by* D.G. Brand. Canadian Forest Service, Petawawa National Forestry Inst., Chalk River, Ontario, Canada. pp. 119-129.

Pureswaran, D.S., De Grandpré, L.D., Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., and Kneeshaw, D.D. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. Ecology **96**(6): 1480-1491.

Remsoft Inc. 2008. Spatial Woodstock 2008.12 user guide. Remsoft Inc., Fredericton, New Brusnwick, Canada p.

Robert, L.-E., Kneeshaw, D., and Sturtevant, B.R. 2012. Effects of forest management legacies on spruce budworm (*Choristoneura fumiferana*) outbreaks. Can. J. For. Res. **42**(3): 463-475.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec mériodional. Direction de la gestion des stocks forestiers et direction des relations publiques, ministère des ressources naturelles. Publications du Québec, Québec.

Roland, J., and Taylor, P.D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature **386**(6626): 710-713.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. Ecol. Monogr. **54**(4): 429-462.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, New York.

Ruel, J.C., and Huot, M. 1993. Impact de la tordeuse des bourgeons de l'épinette [*Choristoneura fumiferana* (Clem.)] sur la régénération des sapinières après la coupe à blanc. The Forestry Chronicle **69**(2): 163-172.

Sainte-Marie, G.B., Kneeshaw, D., and MacLean, D.A. *In prep*. Relative impacts of forest harvesting and spruce budworm on forest composition 30 years after an outbreak.

Sainte-Marie, G.B., Kneeshaw, D.D., MacLean, D.A., and Hennigar, C. 2015. Estimating forest vulnerability to the next spruce budworm outbreak: Will past silvicultural efforts pay dividends? Can. J. For. Res. **45**: 314-324.

Sauvageau, F. 1995. Silvicultural terms in Canada. Second (revised) edition. Canadian Forest Service. *In* Natural Resources Canada, Ottawa, Ontario, Canada p.

Scheller, R., Domingo, J., Sturtevant, B., Williams, J., Rudy, A., Gustafson, E., and Mladenoff, D. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Model. **201**(3-4): 409-419.

Scheller, R.M., and Mladenoff, D.J. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol. Model. **180**(1): 211-229.

Schoemaker, P. 1995. Scenario planning: a tool for strategic thinking. Sloan Management Review(winter): 25-40.

Senecal, D., Kneeshaw, D., and Messier, C. 2004. Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Can. J. For. Res. **34**(2): 396-404.

Spence, C.E., and MacLean, D.A. 2012. Regeneration and stand development following a spruce budworm outbreak, spruce budworm inspired harvest, and salvage harvest. Can. J. For. Res. **42**(10): 1759-1770.

Sturtevant, B., Cooke, B., Kneeshaw, D., and MacLean, D. 2015. Modeling Insect Disturbance Across Forested Landscapes: Insights from the Spruce Budworm. *In* Simulation Modeling of Forest Landscape Disturbances. *Edited by* A.H. Perera and B.R. Sturtevant and L.J. Buse. Springer International Publishing. pp. 93-134.

Sturtevant, B.R., Gustafson, E.J., Li, W., and He, H.S. 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecol. Model. **180**(1): 153-174.

Su, Q., MacLean, D.A., and Needham, T.D. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can. J. For. Res. **26**(9): 1620-1628.

Thompson, D.G., and Pitt, D.G. 2003. A review of Canadian forest vegetation management research and practice. Annals of Forest Science **60**(7): 559-572.

Vérificateur général du Québec. 2002. Rapport à l'Assemblée nationale pour l'année 2001-2002. Tome II. Bibliothèque nationale du Québec.

Wagner, R.G., Little, K.M., Richardson, B., and Mcnabb, K. 2006. The role of vegetation management for enhancing productivity of the world's forests. Forestry **79**(1): 57-79.

Wang, W.J., He, H.S., Fraser, J.S., Thompson, F.R., Shifley, S.R., and Spetich, M.A. 2014. LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. Ecography **37**(3): 225-229.

White, J.A., and Whitham, T.G. 2000. Associational susceptibility of cottonwood to a box elder herbivore. Ecology **81**(7): 1795-1803.